Browse Availability, Bite Size, and Effects of Stand Age on Species Composition and Browse Density for Moose in Northeastern Minnesota

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Abstract

Large ruminant herbivores like moose spend most of their time foraging and ruminating to acquire and process enough plant biomass to meet energy and nutrient requirements. In northeastern Minnesota, moose forage in a mosaic of forest stands with ages shaped by harvest and other disturbances. Distribution and abundance of browse species varies across the landscape and each browse species has unique growth patterns and a patchy distribution within and among different stand types. To estimate available and consumed biomass, we collected available twigs and created diameter-at-point-of-browsing–biomass regressions for each browse species. These relationships varied by canopy closure and were used to estimate biomass consumed on foraging paths. We also measured browse availability and use along foraging paths of GPS radio-collared moose and within randomly selected regenerating stands in northeastern Minnesota. We measured all sites using traditional methods and a method that simulates moose foraging behavior by measuring large feeding stations. We tested the hypotheses that (1) browse density is higher at large feeding stations than at random locations along a foraging path, (2) browse density is higher at large feeding stations than at randomly chosen feeding stations along a foraging path, and (3) browse density is higher at large feeding stations than along a straight transect. At each site we measured available species composition, available browse density, diet composition, and browse species selection. Combined with the use of GPS collars this method allowed us to compare the foraging path diet composition and browse selection of individual free-ranging moose. Paper birch, willow, and quaking aspen were common in young stands while hazel, mountain maple, and balsam fir (winter) or juneberry (summer) were common in older stands. Browse density also changed with stand age, but the changes in species composition and browse density were similar along foraging paths and within randomly selected regenerating stands indicating that moose habitat restoration projects can effectively create forage for moose. In areas with and without collared moose the simulated browsing method was an effective tool for measuring browse availability and use. We also provide evidence from the field that moose, and possibly other large herbivores, obtain most of their energy intake from small patches of high density browse.

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Introduction

Large herbivores like moose (*Alces alces*) view their food resources across the landscape within patches and feeding stations (Senft et al. 1987). A feeding station is a plant or clump of plants with browsed twigs that are accessible when the forefeet of the moose are stationary (Goddard 1968, Novellie 1978, Senft et al. 1987). A patch is a community of similar plants (Senft et al. 1987) within a stand (geographically defined by the extent of disturbances). At the landscape level browse density varies among stands and at patches within stands. Moose choose which patches they will visit based on the spatial distribution of forage resources. Within a patch moose must choose which feeding stations to visit based on the available browse species and the ages of trees and shrubs the feeding stations contain. Younger stands and patches can provide large quantities of high quality browse while older stands and patches with trees which have grown out of reach of moose provide less browse (Schwartz 1992). Within both the patch and feeding station, bite size is based on the tradeoff between cropping and processing (Spalinger and Hobbs 1992).

Moose need to consume about 130 g dry mass/kg body weight$^{0.75}$ daily in summer and about 40 g dry mass/kg body weight$^{0.75}$ daily in winter (Renecker and Hudson 1985). This corresponds to a daily intake requirement of about 13 kg in summer and about 4 kg in winter for a 454 kg (1000 lb.) moose. This large demand for forage forces moose to move frequently between patches and feeding stations in order to consume enough biomass. While at a feeding station moose preferentially browse more nutritious small diameter twigs and gradually switch to less nutritious, larger diameter, as the smaller twigs are exhausted. During the time spent browsing twigs at one feeding station a threshold is reached where the net energy gained by moving to a new feeding station is

greater than the net energy gained by continuing to browse at the original feeding station and browsing large diameter twigs. When this threshold is reached the moose should move to the next feeding station (Spalinger and Hobbs 1992). However, when the distance between feeding stations becomes large, moose may continue to browse on twigs with larger diameters (Spalinger and Hobbs 1992).

Moose complete several foraging bouts each day to meet their energy requirements. In summer moose consume leaves of deciduous species which are relatively easily digested (Schwartz and Renecker 1997) and available. Therefore, moose can consume large quantities of browse in summer. Because one bite is approximately 1 g dry mass (Renecker and Hudson 1986) approximately 13,000 bites are eaten per day in summer by a 454 kg moose.

In the winter moose browse on twigs of deciduous species and needles and twigs of conifers. These plant parts have a lower net energy gain than deciduous leaves due to the larger proportion of structural carbohydrates (Moen 1985). Current annual growth of twigs is more digestible than the previous year's growth (Schwartz 1992). In winter a 454 kg moose needs approximately 4 kg of browse per day and one bite is approximately 1 g dry mass (Renecker and Hudson 1986). This corresponds to about 4,000 bites per day in winter.

Browse availability and bite size have been measured by following either moose or moose tracks in the snow and counting the number of available twigs of each species, the number of bites of each species, and measuring diameter-at-point-of-browsing, dry mass, and twig length (Risenhoover 1987, Hjeljord et al. 1990, Shipley et al. 1998). Locations of moose were found via radio telemetry (Risenhoover 1987, Hjeljord et al. 1990) or

finding a moose track crossing a road (Shipley et al. 1998). These methods were both largely opportunistic and data collection was either clumped temporally (location every hour for two days) or spread widely temporally (1-2 tracks per week).

Another typical method is to measure browse availability in plots along randomly placed transects instead of following moose foraging paths. This is a statistically sound way to measure potential browse availability and distribution of browse species. However, we tested a method of measuring browse availability and use by attempting to simulate how a moose perceives browse. We used GPS collars to follow moose movements and locate foraging paths in both summer and winter.

Given that we could locate foraging paths we tested three hypotheses: (1) browse density is higher at large feeding stations than at random locations along a foraging path, (2) browse density is higher at large feeding stations than at randomly chosen feeding stations along a foraging path, and (3) browse density is higher at large feeding stations than along a straight transect. In the future this method could be used to estimate browse availability in areas within moose range that do not have collared moose.

Study Area

This study was conducted in northeastern Minnesota where moose had been previously collared for a VHF telemetry study (Fig. 1.1) (Lenarz et al. 2010). The study was in the Laurentian Great Lakes Forests which are between the Canadian boreal forests and the northern hardwood forests and experience a continental climate with short warm summers and severe winters (Heinselman 1996). Most of the land ownership was in the Superior National Forest. The remaining land in the study area was in state, county, tribal, or industrial ownership (Moen et al. 2011, Lenarz et al. 2010). Details on the study

area and location in relation to the other Minnesota moose projects can be found in the Minnesota Moose Research and Management Plan (MNDNR 2011).

Methods

Regressions and Estimating Bite Mass

In order to create diameter-at-point-of-browsing–biomass regressions to assist in measuring browse biomass along foraging paths we clipped browsed twigs of all browse species (Table 1.1) approximately 3 cm below the browse point using garden clippers and placed them in a bag labeled with the location, date, and species. In summer we collected stripped twigs of each species which we clipped directly above the first unbrowsed petiole. We also collected unbrowsed twigs of each browse species in various locations within the study area throughout the winter and summer to develop diameter-at-point-of-browsing–biomass regressions for each season (Telfer 1969, Peek et al. 1971, MacCracken and Viereck 1990, MacCracken and Van Ballenberghe 1993). In winter a bite was the biomass of a twig with a current annual growth longer than 5 cm and in summer a bite was the leaf biomass from one twig with a current annual growth longer than 5 cm.

All browsed and unbrowsed twigs and leaves were stored at 2-3 degrees Celsius until measurements were taken. On the browsed twigs we measured the diameter-at-point-of-browsing to the nearest 0.01 mm. On the unbrowsed twigs we measured the simulated diameter-at-point-of-browsing to the nearest 0.01 mm. In winter we clipped each collected twig at one point along the current annual growth and the simulated diameter-at-point-of-browsing was measured right above the cut. In summer the simulated point of browsing was the diameter below the last petiole we stripped. We measured a range of

diameters in both seasons for the simulated browse twigs. In winter the wet mass of each unbrowsed twig was measured to the nearest 0.01 g. In summer the wet mass of the stripped leaves of unbrowsed twigs was measured to the nearest 0.01 g. Every unbrowsed twig in both seasons was stored in a labeled bag. In summer the leaves were placed in the same bag as their corresponding twig after the wet mass of the leaves was recorded.

All unbrowsed summer and winter twigs were dried at 60 degrees Celsius for 48 hours. Dried twigs in winter and leaves in summer were stored at room temperature until measured to the nearest 0.01 g. Most winter twigs (74%) and summer leaves (90%) were measured within five days of removal from the drying oven. The remaining twigs and leaves were measured six to nine days after removal from the drying oven.

We collected simulated summer moose bites between July and September 2012. This longer period of collection may have introduced some variation in leaf biomass and twig diameter. We assumed most plant growth was complete and most leaf mass was present by mid-July. Therefore, we combined data from July to September for each regression. In winter twigs were collected between January and April of 2012 and 2013. Plants do not grow in winter so collecting between January and April would not affect the twig mass and twigs from both years were combined for each regression.

GPS Collars

We captured adult moose in February and early March 2011 by darting them from helicopters (Quicksilver Air, Inc., Fairbanks, AK). Moose were sedated with 1.2 ml (4.0 mg/ml) carfentanil citrate and 1.2 ml (100 mg/ml) xylazine HCl. GPS collars (Sirtrack Ltd and Lotek Wireless) were fitted to each moose and were programmed to transmit a location every 20 minutes. We used 7.2 ml (50 mg/ml) naltrexone HCl and 3 ml (5

mg/ml) yohimbine HCl as an antagonist. Animal capture and handling protocols met the guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011) and were approved by University of Minnesota and National Park Service Animal Care and Use committees.

Measuring Browse Availability

Summer browse availability was measured between 25 July 2012 and 14 September 2012. Winter browse availability was measured between 3 January 2013 and 22 March 2013. Browse availability was measured at the patch scale. We used the GPS collar locations to identify areas with a concentrated number of locations indicating foraging activity where we were likely to find foraging paths. A foraging path was considered a trail of feeding stations. Summer foraging paths were measured 1 to 15 days after the moose departed. Winter foraging paths were measured 3 to 17 days after the animal had departed. We measured paths within this time range to ensure the foraging paths were recent enough that we could find them by following tracks in snow, broken twigs, and/or feeding stations. It is possible, but we believe unlikely, that we combined two foraging paths into one. Sites were considered accessible if they were on public land and we could reach them by walking less than 2 km on a trail and/or less than 550 m off a trail. Foraging paths of eight moose were measured in winter (6 female and 2 male) resulting in a total of 29 different sites. In summer 31 foraging paths of seven moose were measured (5 female and 2 male). We used a Garmin GPS to reach moose locations on foot and then searched for feeding stations forming a foraging path.

We defined a large feeding station as a feeding station that appeared to have ≥10 bites. At all sites we measured browse using four different protocols: (1) large feeding stations

only; (2) random plots along the foraging path; (3) random feeding stations along the foraging path; (4) plots along a straight transect through the area of the foraging path. Each path type consisted of ten plots.

The first large feeding station we encountered was the first large feeding station plot and the first plot of the site. A plot represented a feeding station as a half circle with a radius of 99.1 cm (39 inches). The center of the straight side of the half circle plot was held at the approximate place where the moose stood. Moose tracks in winter, and other signs present in either season, were also used to determine where the moose stood. This first feeding station was marked with a waypoint on a Garmin GPS. At each feeding station we counted the unbrowsed and browsed twigs of each browse species between 0.5 and 3 m above the ground (Table 1.1; Shipley et al. 1998). Each twig was considered a bite. Occasionally an assumed large feeding station had fewer than 10 bites. The twig counts from that plot were still used as a large feeding station because the feeding station looked like it offered more than ten bites. This occurred in 10 of 290 large feeding stations in winter (3%) and in 36 of 297 large feeding stations in summer (12%).

After measuring the first feeding station we followed the foraging path using tracks and signs of browsing to locate the next large feeding station, marked it as the second waypoint on the GPS, and counted available and browsed bites (Fig. 1.2). Plots could not overlap and this process was continued until 10 large feeding stations had been measured.

In addition to measuring the large feeding stations we stopped at predetermined random distances along the foraging path and measured a plot at that location. These plots were termed “random plots” and made up the random plot path. We randomly

assigned a distance of 5 to 14 m between plots. In the field we measured the distance walked from the last random plot using the GPS "find" feature (Fig. 1.2).

We completed a third path type of random feeding stations. Random feeding stations were identified based on the random plots. If a random plot had bites taken in it, then that random plot also counted as a random feeding station. However if there were no browsed bites in the random plot, we followed the foraging path to the nearest browsed twig (even if only one bite) and this was the location of the random feeding station (Fig. 1.2).

After 10 large feeding stations, 10 random plots, and 10 random feeding stations had been measured we completed a straight transect that returned to the first plot. Along the straight transect we stopped at predetermined random distances and measured a plot at that location until ten plots were completed. We randomly assigned a distance of 5 to 14 m between plots. If we reached the first large feeding station plot before we had completed ten straight transect plots we continued along the straight line past the first plot. If the cover type changed after passing the first large feeding station plot and we needed to complete more straight transect plots we angled to remain in the same cover type. In winter 10 of 29 straight transects were angled a mean of 75 degrees (SE = 24 degrees). In summer 15 of 31 straight transects were angled a mean of 80 degrees (SE = 11 degrees).

Some cover types had little available browse making the foraging path difficult to follow. If no bites were found within 20 meters of the last measured feeding station when moving in a forward direction we assumed the moose stopped foraging and there were fewer than 10 large feeding stations, random feeding stations, and/or random plots in that foraging path. In the summer 20 of 30 foraging paths had ten plots in all path

types. In winter the tracks in the snow allowed us to follow the trail without seeing the bites immediately from the previous feeding station and aided in completely measuring an entire foraging path. Thus, in the winter 28 of 30 foraging paths had 10 plots in all path types.

Canopy cover was measured after every eighth plot at each site using a densiometer. Three densiometer readings were completed at each foraging path and averaged. Twigs taken from sites with 0-50% canopy closure were considered grown in open canopy and twigs from sites with 70-100% canopy closure were considered grown in closed canopy. Twigs taken from sites with 51-69% canopy cover were not used in the regressions or bite size summary statistics.

Statistical Analyses

Diameter-at-point-of-browsing–biomass regressions, ANOVAs and Tukey-Kramer HSD *t*-tests on browse density, Kruskal-Wallis comparisons of diet, Pearson χ^2 Goodness of Fit tests, and Bonferroni Z-tests were all performed in Jmp 10.0. Significance level was set at 0.05.

Regressions

Simulated diameters at point of browsing and dry masses of twigs from the unbrowsed winter twigs were base-10 log transformed and used to make two separate diameter-at-point-of-browsing–biomass regressions for each of the main browse species. The first regression used twigs grown in open canopy (0-50% shaded) and the second used twigs grown in closed canopy (70 -100% shaded). Regressions for open and closed canopy were also made for each browse species in summer when the dry mass was comprised of leaves only.

Summary statistics on bite size diameter and bite mass were calculated for each species. A *t*-test was used to test for differences between the mean diameter-at-point-of-browsing in open and closed canopy in both seasons for each species.

Available browse density

Browse density was estimated two ways. The first method was twig counts and the second was biomass. To obtain the total number of available twigs per path we added the number of available twigs and the number of browsed bites. We estimated the total biomass available (or consumed) along a foraging path by multiplying the number of twigs available (or consumed) of a given species by the mean biomass of one bite of that species. For foraging paths in 0-50% shade we used the mean biomass values from open canopy regressions. For foraging paths in 51-100% shade we used the mean biomass values from closed canopy regressions. Although the closed canopy regressions were made using twigs grown in 70-100% shaded areas, we felt the foraging paths in 51-69% shade were better classified as closed canopy than open canopy. Balsam fir was not included in summer browse density estimates because it is not a part of the diet in summer.

Available browse density and consumed browse density within each path type were estimated using twig counts and biomass in both seasons. The area covered by the foraging path was calculated by measuring the distance from the first plot of a path type through all plots of that path type to the last plot of the same path type. This distance was then multiplied by two to represent the ability of the moose to browse on either side of the foraging path. We then divided the twig count (available or consumed) by the area of the foraging path to calculate browse density. These same calculations were made

using biomass instead of twig counts. The browse density of large feeding station paths was compared to the browse density of random feeding station paths, random plot paths, and straight transects by performing an ANOVA on the log transformed data.

Diet composition

Diet composition was calculated for each moose at the four path types in both seasons. We took a weighted mean of those diet compositions to estimate diet composition for all moose at each path type in winter and summer. Species were considered rare when they made up less than 1% of the averaged diet (Shipley et al. 1998) at large feeding station paths. The percentage of the diet consisting of rare species is reported in the tables to show when a few individuals consumed large quantities. However, because the rare species contributed a very small portion to the diet when considering all moose, the text does not include results about the rare species.

Because moose never ate all the species available in the study area, every moose's diet had at least one browse species at zero percent. Because this data was skewed and no transformations could correct this skewedness we used a Kruskal-Wallis test to test for significant differences among diet compositions at the four path types. A Kruskal-Wallis test was also used to test for significant differences between each individual moose's diet.

Browse species selection

We also determined the selection for each browse species in NE MN for all moose combined and for each individual using the data from large feeding station paths. A Pearson χ^2 Goodness of Fit test and a Bonferroni Z-test were performed on the availability and use of all browse species for all moose combined and each individual moose (Neu et al. 1974). A species was considered positively selected if there was a

significantly larger proportion of browsed twigs of a particular species than the proportion of the available twigs of that species. A species was considered avoided if there was a significantly smaller proportion of browsed twigs of a species than the proportion of available twigs of that species. A species with non-significantly different percentages of use and availability was considered neutral.

Results

All of the twig diameter-at-point-of-browsing–biomass regressions had slopes significantly different from zero (Tables 1.2 and 1.3). In winter 75% of the regressions had an $R^2 > 0.60$ and in summer 43% had an $R^2 > 0.60$. Slopes of regressions for open canopy twig samples were not consistently greater than slopes for closed canopy twig samples, but the relationship with canopy cover varied by species. In winter and summer mountain maple (*Acer spicatum*), paper birch (*Betula papyrifera*), red-osier dogwood (*Cornus stolonifera*), and willow (*Salix* spp.) all had larger slopes in open canopy than in closed canopy and juneberry (*Amelanchier* spp.), quaking aspen (*Populus tremuloides*), and mountain ash (*Sorbus decora*) had higher slopes in closed canopy than in open canopy.

Bite Size

Mean (± SE) diameter-at-point-of-browsing in winter across all species was 3.0 ± 0.02 mm in open canopy (range: 0.5 to 9.0 mm) and 3.1 ± 0.1 mm in closed canopy (range: 0.2 to 8.4 mm; Table 1.4). In summer the mean diameter across all species was 2.3 ± 0.02 mm in open canopy (range: 0.02 to 11.1 mm) and 2.4 ± 0.04 mm in closed canopy (range: 0.2 to 6.1 mm; Table 1.5). Using the regressions (Tables 1.2 and 1.3) we calculated the mean biomass consumed per bite for each browse species (Tables 1.4 and

1.5). Pin cherry (*Prunus pennsylvanicus*) in closed canopy had the largest bite in winter (2.3 ± 1.4 g) and the smallest bite in winter occurred in pin cherry (0.4 ± 0.1 g) in open canopy and mountain maple in closed canopy (0.4 ± 0.2 g). The largest bite in summer was mountain ash in closed canopy (1.7 ± 1.4 g) and the smallest was quaking aspen in closed canopy (0.3 ± 0.2 g).

Large Feeding Station Method

The purpose of the random feeding station paths was to estimate the frequency at which feeding stations of different sizes (numbers of consumed bites) occurred. In winter 161 of the 281 random feeding stations measured (57%) were large (10+ bites). However, 86% of the 3,742 browsed twigs counted at all random feeding stations were at random feeding stations with ≥10 bites (Fig. 1.3). In summer 131 of the 267 random feeding stations (49%) were large (≥10 bites). Yet 82% of the 3,446 browsed twigs counted at all random feeding stations were taken from random feeding stations with ≥10 bites (Fig. 1.3). In both seasons along the random feeding station paths at least 80 percent of the browsed twigs were at random feeding stations we considered to be large (≥10 bites).

Browse Density

Total available browse density was measured two different ways in winter (n = 29) and summer (n = 30): available number of twigs and available biomass. The available browse density was significantly different between the four path types in both seasons using both methods (winter twigs $F_{3, 112} = 62.7$, summer twigs $F_{3, 118} = 32.5$, winter biomass $F_{3, 112} = 84.3$, summer biomass $F_{3, 120} = 16.8$, $P_{all} < 0.0001$; Table 1.6). Consumed browse density was also significantly different between the four path types by

number of twigs and biomass in winter and summer (winter twigs $F_{3, 112} = 63.4$, summer twigs $F_{3, 120} = 31.2$, winter biomass $F_{3, 112} = 70.9$, summer biomass $F_{3, 119} = 5.0$, $P_{all} < 0.0025$).

Both available and consumed browse densities were highest at large feeding station paths, followed by random feeding station paths, random plot paths, and finally straight transects when estimated by both twig counts and biomass (Table 1.6). In both seasons there was always a higher density of available browse at large feeding stations than at the other three path types (Tukey-Kramer HSD, $P_{all} < 0.014$) when measured by twigs/m^2 and biomass/m^2. This was also true for consumed density, with the one exception that consumed summer density by biomass at large feeding stations was not significantly different from random feeding stations (Tukey-Kramer HSD, $P = 0.18$).

The mean distance walked to complete the 10 large feeding stations plots in winter (27.6 ± 2.0 m, n = 29) was about half the distance to complete 10 large feeding station plots in summer (50.5 ± 4.9 m, n = 31). In winter large feeding station paths had a mean of 727 ± 31 twigs (471 ± 26 g) available whereas in summer 460 ± 37 twigs (1166 ± 88 g) were available.

The available and consumed browse densities were also calculated for each browse species. Available and consumed browse densities for each browse species was largest at large feeding station paths followed by random feeding station paths, random plot paths, and straight transects. The one exception was the estimate of available browse density of hazel in summer based on twig counts. Hazel in summer had the highest available browse density estimated by the straight transect, followed by large feeding stations,

random plots, and then random feeding stations when estimated by number of twigs. However, hazel was rarely consumed in summer.

Percent Consumed

At large feeding stations 35% of the available twigs in winter were browsed (Table 1.7). In summer 45% of the available twigs at large feeding stations were browsed. The percentage of the available twigs consumed decreased from large feeding station paths to random feeding station paths, then random plot paths and finally straight transects. At straight transects 13% of the available twigs were consumed in winter and 9% of the available twigs were consumed in summer.

Diet Composition

Season

In winter when data from all moose were combined at least 70% of the bites consumed along all four path types consisted of hazel (*Corylus cornuta*), paper birch, willow, and quaking aspen (Table 1.8). The remaining 30% of the consumed bites at all four path types were balsam fir (*Abies balsamea*), juneberry, mountain maple, red maple (*Acer rubrum*), red-osier dogwood, pin cherry, and choke cherry (*Prunus virginianus*). In winter the rare species were alder (*Alnus rugosa*), mountain ash, balsam poplar (*Populus balsamifera*) and white pine (*Pinus strobus*) (Table 1.8).

Diet composition at foraging paths varied between seasons. Along large feeding station paths, random feeding station paths, and random plot paths 70% of the bites in summer consisted of mountain maple, willow, and paper birch (Table 1.9). Species making up the remaining 30% of the consumed bites in summer along those three path types were juneberry, red maple, pin cherry, choke cherry, quaking aspen, and mountain

ash. Rare species in the summer were hazel, balsam poplar, red-osier dogwood, balsam fir, alder, bog birch (*Betula pumila*), black ash (*Fraxinus niger*), oak (*Quercus* spp.), elderberry (*Sambucus pubens*) and white pine. Along straight transects in summer 72% of the consumed twigs were mountain maple, willow, quaking aspen, and species considered rare (those species individually making up <1% of the diet along the large feeding station paths) (Table 1.9).

Path type

Despite the general similarities in diet diversity, all browse species comprised significantly different portions of the diet in winter among the four path types (Kruskal-Wallis, $H_3 > 12.3$, $P < 0.007$). The two exceptions were paper birch and hazel which was not different between the four path types (Kruskal-Wallis, $H_3 < 1.2$, $P > 0.60$; Table 1.8).

In summer juneberry, quaking aspen, and mountain ash comprised significantly different portions of the diet at all four path types (Kruskal-Wallis, $H_3 > 8.1$, $P < 0.045$; Table 1.9). There was not a significant difference between the four path types for red maple, mountain maple, paper birch, cherry, and willow (Kruskal-Wallis, $H_3 < 5.7$, $P > 0.13$).

Individuals

The percent of each browse species consumed along foraging paths varied among individual moose in both winter and summer. Based on the twigs consumed at large feeding stations each moose's diet along these foraging paths varied from the other individuals and also from the pooled mean (Tables 1.10 and 1.11). One example of the individual differences in winter was female moose 31180. In the four foraging paths we measured of this moose, she consumed 26% red maple and 50% hazel compared to the

weighted mean consumption of all moose of 5% red maple and 27% hazel (Table 1.10). In summer an example of individual differences was male moose 31190 who consumed 10% mountain maple and 61% willow in the four foraging paths we measured compared to the weighted mean of 41% mountain maple and 21% willow (Table 1.11). These differences in diet are a biologically relevant difference in both seasons.

Browse Species Selection

In winter browse species were eaten at proportions significantly different than expected when the diets of all moose were averaged (χ^2_{10}= 3122, $P < 0.0001$). We considered the proportional availability of each species to be the expected proportion in the diet. A Bonferroni Z-test on the combined data showed juneberry, red maple, mountain maple, paper birch, red-osier dogwood, and quaking aspen were eaten in summer significantly more than they were available. Hazel and balsam fir were eaten significantly less often than they were available and the amount of cherry and willow browsed did not differ significantly from their availability (Table 1.12). Additionally, when each moose was evaluated independently their diets were significantly different than the availability at their foraging paths ($\chi^2 > 74.6$, $P < 0.0001$ for all moose).

In summer when the diets of all moose were averaged browsed species were again consumed at significantly different levels than expected according to availability (χ^2_{10} = 840, $P < 0.0001$). This was also true when each individual moose was evaluated separately (all moose had $\chi^2 > 43.9$, $P < 0.0001$). A Bonferroni Z-test on the combined data showed red maple, mountain maple, cherry, and mountain ash were eaten significantly more than they were available in summer (Table 1.12). Willow was eaten significantly less than it was available. Juneberry, paper birch, and quaking aspen did not

have a significant difference between the percent they were available and the percent they were browsed (Table 1.12).

Discussion

Browse density at large feeding station paths was significantly greater than at the three other path types supporting all three of our hypotheses. First, because the density at large feeding station paths was greater than at random plot paths, moose actively chose feeding stations and did not stop at random along a foraging path to browse. Second, the density at large feeding station paths was greater than at random feeding station paths indicating that moose chose feeding stations along the foraging path that had a higher density of twigs. Finally, the browse density of large feeding station paths was greater than at straight transects indicating that deviating from a straight line when browsing effectively increased browse intake.

This provides evidence that moose make decisions at multiple scales when browsing that effectively increase their browse intake compared to foraging at random. Our data indicates that (1) moose forage along paths that offer significantly more twigs/m^2 than foraging at random, (2) moose obtain at least 80% of their forage from large feeding stations, and (3) moose also select certain species over others within a feeding station. This provides evidence based on field measurements that moose forage with a Type II functional response (Spalinger and Hobbs 1992). We think the foraging behavior results would be similar in many other herbivores with a Type II functional response. These results also support using the large feeding station method we have proposed to measure browse availability and browse consumption by herbivores with a Type II functional response.

Additionally, by measuring foraging paths (or simulated foraging paths) this method measures browse availability and use differently than straight transects and avoids two complications present in the straight transect method. First, straight transects are better for measuring browse availability than browse consumption while our method effectively measures both. Second, plots in straight transects are often empty. Empty plots create problems for statistical analyses and are also an unrealistic measurement of browse availability when browse occurs in patches. A moose would not stop in the middle of an empty area to browse. Instead, the moose would continue walking until reaching available browse. By only stopping at large feeding stations our method avoids the complications of empty plots and provides an estimate of effective browse density.

Along foraging paths the diet composition was statistically different among seasons and path types. The mean diet in both winter and summer at these foraging paths was best categorized as generalist because one genus did not account for >60 % of the diet (Shipley 2010). The two species composing the highest proportions of the winter diet were beaked hazel and paper birch while the two species composing the highest proportions of the summer diet were mountain maple and willow. Additionally, willow was a large portion of the browse consumed by uncollared moose in the Greenwood Lake area in winter, so it is likely that willow is more important to moose in this area than the other data indicates. The seasonal differences are biologically relevant because they reflect the changing nutritional qualities and digestibility in each species throughout the year. Additionally, moose may be choosing to forage in different areas in winter and summer. Future research using collared animal locations could try to distinguish seasonal

differences in foraging locations and if those areas provided different browse species availability.

The diet composition we measured was similar to previous diet composition estimates in NE MN (Peek et al. 1976; Table 1.13). In summer the top five species ranked by percent of the diet were the same in both studies: mountain maple, willow, paper birch, cherry, and quaking aspen. However, mountain maple was ranked first in our study and fifth in the Peek et al. (1976) study while quaking aspen had the opposite rankings (Table 1.13). In winter hazel, willow, and quaking aspen were considered three of the top five species in both studies. However, our data indicated that paper birch and juneberry were also in the top five species while Peek et al. (1976) found that balsam fir and red-osier dogwood were in their top five species.

Within both seasons the main species consumed were consistently important regardless of path type. However, the number of twigs counted by the large feeding station paths was greater and captured a more complete estimate of the species consumed by moose. This provides additional support for using the large feeding station method we have proposed because it does not require counting every single twig, but still gives an accurate estimate of browse intake rates, consumed browse composition, and browse species selection.

This study was unique because we were able to collect data at foraging paths of known individual free-ranging moose. The difference between individual diets can be highlighted by the two moose that were considered specialists in summer (31178 and 31175) and moose 31190 that was a specialist in both seasons (Tables 1.10 and 1.11). Although no previous studies have reported diet selection among individuals, differences

in habitat selection between individual moose were found in British Columbia (Gillingham and Parker 2010). Pooling the data from many foraging paths provided a generalized view of the most important browse species in NE MN. However, the differences between individual foraging paths indicate there likely is not a singular diet composition that applies to all moose. The variation between individuals also indicates that moose are able to adapt their diet based on the available browse species in a given area. Managers can consider this variety in diet when choosing areas to harvest and burn to create early successional moose habitat, as species composition pre-disturbance has an impact on post-disturbance composition.

Our results also indicate that each individual moose made choices about what to browse in each location instead of only taking what is available. This provides additional support for our large feeding station method because this method reflects the moose's experience more realistically. A challenge to "pretending" to be a moose when following a foraging path is that humans find large feeding stations by sight, but a moose may be using additional senses. However, our method remains more realistic than a straight transect.

Our regressions for each browse species were stronger predictors when divided by canopy and season than when only divided by season. Thus, future researchers estimating consumption based on number of twigs consumed, will obtain the most accurate results when browse species, season, canopy cover, and geographic location are all considered in their regressions. Diameter-at-point-of-browsing–biomass regressions have been created before for winter twigs in NE MN (Peek et al. 1971) and for winter twigs and summer leaves in the Copper River Delta of Alaska (MacCracken and Van Ballenberghe 1993).

While none of the Minnesota regressions were transformed and some of the Alaska regressions had transformations, all of ours needed to be base-10 log transformed. Although we had a large range in R^2 values for our regressions, 75% of our regressions in winter and 43% in summer had an $R^2 > 0.60$. In comparison, Peek et al. (1971) did not report R^2 values and MacCracken and Van Ballenberghe (1993) reported five of 14 regressions (35%) with an $R^2 > 0.60$.

The mean available browse density estimated by biomass at large feeding stations was higher in summer than in winter as expected (Table 1.6). In contrast, available browse density estimated by twig counts was greater in winter than in summer. There are two possible explanations for this. First, there were a greater number of available twigs in winter than in summer because different species were counted as "common browse species" in each season. Second, hazel was used often in winter but rarely in summer along our foraging paths and due to the branching growth pattern of hazel it is possible to get very large estimates of available twigs at one feeding station. However, hazel is readily abundant year-round and may be consumed in greater quantities elsewhere in summer which could possibly even out the differences presented here.

Along the foraging paths we measured, consumption of available twigs was high at large feeding station paths (35-45%) indicating that moose consume large portions of available browse at the feeding station scale. Within the same stands consumption was 9-13% at straight transects indicating that moose consume significant portions of available twigs at the stand scale. This could potentially reduce browse availability in future years at the foraging path and stand scales (De Jager et al. 2009).

This raises questions about browse density at the landscape scale in northeastern Minnesota. Browse density varies across the landscape based on stand age, tree species composition, and geographic features. We estimated browse density by measuring stands where moose chose to spend time. These patches were likely areas with high browse density which provide us with an estimated browse density for those areas where moose are likely to forage. However, moose are generally believed to be an early successional species (Peek 1974, Peek et al. 1976, Lenarz et al. 2011) and forest harvest has decreased in the past decade in northeastern Minnesota (Wilson and Ek 2013) which could be decreasing beneficial moose habitat. To estimate density across moose range in northeastern Minnesota we would need to measure density in all patch types (not just where foraging paths are present) and use ArcGIS, date of harvest, and satellite imagery, to analyze how much of the landscape is occupied by stands of different ages to extrapolate density to the landscape scale.

Chapter 2: Effects of Stand Age on Species Composition and Browse Density in Northeastern Minnesota

Introduction

Moose (*Alces alces*) spend large portions of their day foraging. During this time they are making decisions on which stands and feeding stations to visit (Senft et al. 1987). Moose choose where they will forage based on the spatial distribution of forage resources. At the landscape level moose will choose among younger stands that can provide large quantities of high quality browse and older stands that have grown out of reach of moose and provide less browse (Schwartz 1992, Peek 1997). At the stand level moose choose which feeding stations to visit based on the available browse species and tree and shrub ages at different feeding stations (Senft et al. 1987, Danell et al. 1991, Pastor and Danell 2003).

Repeated browsing on plants causes hedging which will keep browse within reach of moose and indicates that moose have used the same stands in consecutive years. A spatial memory would make it possible for moose to return to the same stands over multiple years. These stands could be more appealing for foraging because of browse availability, browse quality, browse species composition, predator avoidance, or canopy cover choices. Because repeated browsing can have negative consequences on the quality and quantity of future browse (Pastor and Danell 2003, De Jager et al. 2009, Pastor and De Jager 2013) it is beneficial to compare qualities of foraging sites and non-foraging sites to identify which factors may be influencing moose visitation and foraging.

Many moose populations occur in boreal forests which historically had large disturbances caused by forest fires, wind throw, insect infestations, and plant diseases (Peek 1997). Moose populations tend to increase following large disturbances presumably because they are using young stands for foraging (Aldous and Krefting 1946,

Hatter 1949, Cowan et al. 1950, Spencer and Chatelain 1953). Since the arrival of Europeans in Minnesota timber harvest has become an increasingly important cause of forest disturbance. Between 1940 and 1995 forest harvest became the most common disturbance in northeastern Minnesota (White and Host 2008).

Post-disturbance stands offer abundant regenerating twigs of deciduous trees and shrubs which constitute most of the moose diet (Courtois et al. 2002). The range of years post-disturbance that offer moose the greatest browse availability varies in the published literature. In Alaska peak browse availability varied between five and 20 years (Spencer and Hakala 1965), 11-30 years (Kelsall et al. 1977), and 20-30 years post-disturbance (Weixelman et al. 1998). In Newfoundland 7-10 years post-disturbance offered the greatest density of twigs (Parker and Morton 1978). This indicates that although moose populations may increase within a few years of disturbances, peak browse availability may not occur until years later. In northeastern Minnesota there has been a decline in forest harvest activity over the past decade (Wilson and Ek 2013) which may be affecting the availability of young habitat with moose forage. However, since we do not know which stand ages provide the most browse for moose in Minnesota it is difficult to interpret what effects a decline in forest harvest may have on moose populations in the region.

Browse density is often measured in square quadrats or along straight transects (Parker and Morton 1978, Cumming 1987, Weixelman et al. 1998, Pastor et al. 1998). These methods are simple to implement and can be standardized across studies. However, they measure the potential distribution of browse availability and can have empty plots or miss evidence of browsing. Other methods that have been used followed moose tracks or

collared moose and counted twigs along the foraging paths (Risenhoover 1987, Hjeljord et al. 1990, Shipley et al. 1998). Following moose requires tracks in the snow and is therefore not a viable option in summer, or it requires collared moose, which can be cost prohibitive or unavailable.

In chapter 1 we found the large feeding station method measured browse availability and use along a foraging path, and browse density was higher using this method than browse density measured using a transect sampling method. Therefore, we wanted to test if this feeding station method (Ward and Moen in review) could be used to measure browse availability within randomly selected regenerating stands without foraging paths. If successful, it would enable measurement of browse availability from the perspective of a foraging moose without the need for collared animals. The hypotheses we tested were: (1) the proportion of available browse species common in the diet along foraging paths would be greater than within randomly selected regenerating stands, (2) the density of available browse species would be greater along foraging paths than within randomly selected regenerating stands, and (3) the density of available twigs would be highest in young stands and decrease with stand age. We also tested for differences in species composition between three age classes.

Study Area

This study was conducted in northeastern Minnesota where moose had been previously collared for a VHF telemetry study (Fig. 2.1) (Lenarz et al. 2010). Our locations spanned from Langley River Road in the southwest to the Sawbill Trail in the northeast. The study was in the Laurentian Great Lakes Forests which transition between the Canadian boreal forests and the northern hardwood forests and experience a

continental climate with short warm summers and severe winters (Heinselman 1996). Forest harvest became common in the study area around 1940 and became the predominant disturbance after 1970 (White and Host 2008). Most of the land ownership was in the Superior National Forest. The remaining land in the study area was in state, county, tribal, or industrial ownership (Moen et al. 2011, Lenarz et al. 2010). Details on the study area and location in relation to the other Minnesota moose projects can be found in the Minnesota Moose Research and Management Plan (MNDNR 2011).

Methods

Foraging Paths

We used GPS collar locations to identify and reach areas with moose foraging (Ward and Moen in review). We measured 29 foraging paths in winter 2013 and 41 foraging paths from summers 2012 and 2013. The age of each stand in which the foraging paths occurred was determined in ArcMap 10.0 using aerial photographs and several coverage layers from which stand age could be obtained (Rack et al. 2007, Stueve et al. 2011, Joyce et al. 2014, MNDNR Data Deli 2012). At all foraging paths we measured browse availability and use within a site following the method outlined in Ward and Moen (in review) that measures a foraging path with a large feeding station path, a random feeding station path, a random plot path, and a straight transect.

We defined a large feeding station as a feeding station that appeared to have ≥10 bites that a moose could have consumed when standing in one location. A random plot was a plot completed at predetermined random distances along the foraging path. A random feeding station was identified based on the random plots and had to have ≥1 bite. If a bite was present in the random plot it was also a random feeding station. If no bites were

taken in the random plot we followed the foraging path to the nearest browsed twig and this was the location of the random feeding station. Straight transect plots were plots completed along a straight transect through the area encompassing the foraging path. Plots in all path types were a half circle with a radius of 99.1 cm (39 inches). We counted all browsed and unbrowsed twigs of each browse species in the plot between 0.5 and 3 m above the ground (Shipley et al. 1998).

Regenerating Stands

We identified all the stands regenerating from forest harvest in the study area between 1 and 32 years old and placed them in one of three age classes: 1-11 years, 12-21 years, or 22-32 years post-disturbance. We randomly selected six stands in the youngest class and 12 stands in each of the older classes to sample. In summer we identified four regenerating stands between 1 and 11 years post-disturbance by driving along roads in the study area and stopping to measure recent cuts. In total, 30 regenerating stands were measured in winter and 27 regenerating stands were measured in summer.

At regenerating stands we used the same method to measure browse availability as along foraging paths. However, we simulated a foraging path by moving from one large feeding station of available twigs of common browse species to the next closest large feeding station until we completed 10 plots each of the large feeding station path, the random feeding station path, and the random plot path. Then we completed a straight transect with ten plots. At regenerating stands we moved at least 10 meters into a stand to avoid being on the edge. If browsed bites fell within a plot at the regenerating stands they were recorded as browsed. We then continued along the simulated path towards the area with the highest density of currently available twigs. In contrast to the methods used

in Chapter 1, we did not explicitly follow foraging paths if one existed in regenerating stands. Fifteen of 30 regenerating stands in winter and seven of 27 regenerating stands in summer had signs of moose browsing.

Field Measurements

Summer browse availability at all regenerating stands and 30 of 41 foraging paths was measured between 25 July 2012 and 14 September 2012. The remaining 11 summer foraging paths were measured between 3 July 2013 and 23 July 2013. Winter browse availability at all foraging paths and all regenerating stands was measured between 3 January 2013 and 22 March 2013. At all foraging paths and regenerating stands canopy cover was measured after the eighth, sixteenth, and twenty-fourth plots using a densiometer and the three densiometer readings were averaged. In 17% of stands there were more than 32 plots measured, but we still measured canopy cover after the eighth, sixteenth, and twenty-fourth plots.

Common browse species were those making up >1% of the diet in either the winter or summer and included mountain maple (*Acer spicatum*), red maple (*Acer rubrum*), juneberry (*Amelanchier* spp.), paper birch (*Betula papyrifera*), red-osier dogwood (*Cornus stolonifera*), pin cherry (*Prunus pennsylvanicus*), quaking aspen (*Populus tremuloides*), and willow (*Salix* spp.) in both summer and winter. Beaked hazel (*Corylus cornuta*) and balsam fir (*Abies balsamea*) were common browse species in winter but not in summer and mountain ash (*Sorbus decora*) was a common browse species in summer but not in winter (Peek et al. 1976, Ward and Moen in review).

In summer the rarely available species were alder (*Alnus rugosa*), bog birch (*Betula pumila*), black ash (*Fraxinus niger*), balsam poplar (*Populus balsamifera*), choke cherry

(*Prunus virginianus*), elderberry (*Sambucus pubens*), oak (*Quercus* spp.) and *Viburnum* spp. In winter the rarely available species also included mountain ash (*Sorbus decora*).

Two browse species, balsam fir and beaked hazel, required special consideration in summer. Balsam fir was not consumed in summer and although beaked hazel is abundant it was only 0.3 percent of the diet in summer in Minnesota and therefore we did not count balsam fir or beaked hazel as available species in summer. If we had treated hazel as a potential common summer species, it would have constituted most of the available species composition. This would not realistically reflect what moose are searching for and eating. Therefore, in summer the 10 required available twigs that defined a large feeding station could not be hazel. For the same reasons, random feeding stations had to have ≥1 available twig of a common summer browse species that was not hazel. However, if a large feeding station or random feeding station had the necessary number of twigs of common browse species, then any hazel also inside that plot was also counted as available.

As in Ward and Moen (in review), if a straight transect was going to leave the cover type by continuing in a straight line, we angled the transect to stay in the same cover type. In winter 12 of 30 straight transects at regenerating stands were angled a mean of 74 ± 10 degrees to remain in the same cover type. In summer 14 of 29 straight transects at regenerating stands were angled a mean of 70 ± 8 degrees to remain in the same cover type.

Statistical Analyses

The distance of each path was calculated in ArcMap 10.0 by measuring the line connecting all plots of a certain path type from first to last. This distance was multiplied

by two to represent the ability of the moose to browse on either side of the foraging path. We calculated the browse density in each regenerating stand at all four path types by dividing the number of available twigs (or biomass) in a path by the area of that path type. Biomass values were calculated using regressions for the study area (Ward and Moen in review). We compared the browse density at regenerating stands to the browse density at foraging paths measured during the same seasonal time periods.

We also calculated the available browse species composition for each regenerating stand at all four path types in both winter and summer and compared it to the available browse species composition at foraging paths. Available species composition was measured by twig counts. We also compared browse density and available species composition among three age classes (1-11, 12-21, and 22-32 years post-disturbance).

Differences in available browse density at foraging paths and regenerating stands were calculated for each path type with a *t*-test in RStudio (v 0.98.501, RStudio Inc. 2013). Differences between the densities of the three age classes and differences between densities measured by the four path types were tested by an ANOVA in Jmp 10.0. Differences in available species composition among foraging paths and regenerating stands and the differences between the species composition at the different age classes were calculated with a Kruskal-Wallis comparison test in Jmp 10.0. Significance level was set at 0.05.

Results

Available Browse Density

The mean distance required to complete ten large feeding stations along foraging paths and within regenerating stands was less in winter (28 ± 2 m and 24 ± 3 m,

respectively) than in summer (40 ± 4 m and 51 ± 5 m, respectively; Fig. 2.2). The mean distance needed to complete ten random feeding stations, ten random plots, and ten straight transect plots was very similar at both foraging paths and regenerating stands in winter and summer (Range: 82 ± 5 to 93 ± 3 m).

The mean available browse density measured by all four path types at foraging paths in winter was not significantly different from regenerating stands (*t*-test, $t_{57} < 0.70$, $P > 0.07$; Table 2.1). When measured by biomass, the mean available browse density measured by large feeding station paths at foraging paths (9.9 ± 1.0 g/m^2) was not significantly different from regenerating stands (14.0 ± 1.7 g/m^2; *t*-test, $t_{57} = 1.81$, $P = 0.08$; Table 2.1). However, there was a significant difference between the browse density at foraging paths compared to regenerating stands measured by biomass/m^2 in winter at the random feeding station paths, random plot paths, and straight transects (*t*-test, $t_{57} > 2.27$, $P < 0.01$, Table 2.1).

In summer the mean available browse density measured by twigs/m^2 by all four path types along foraging paths was not significantly different from the browse density within regenerating stands (*t*-test, $t_{70} < 0.88$, $P > 0.38$; Table 2.1). There was again not a significant difference between the browse density at foraging paths compared to regenerating stands measured by biomass/m^2 in winter at the four path types (*t*-test, $t_{70} < 1.15$, $P > 0.25$, Table 2.1).

Browse density varied significantly among path types at foraging paths and regenerating stands in winter and summer (ANOVA, Foraging Paths Winter $F_{3, 112} > 66.1$; Regenerating Stands Winter $F_{3, 116} > 40.9$; Foraging Paths Summer $F_{3, 164} > 14.8$, Regenerating Stands Summer $F_{3, 116} > 36.3$; all comparisons $P < 0.0001$; Table 2.1).

Regardless of density unit (twigs/m^2 or biomass/m^2) large feeding station paths always had the highest density, followed by random feeding station paths, random plot paths, and straight transects. The density measured by large feeding station paths in winter and summer was approximately five times greater than the density measured using the other three path types.

In winter browse density increased with stand age, but the relationship was weak ($R^2 < 0.10$; Fig. 2.3). When winter browse density at regenerating stands was averaged in three age classes (1-11, 12-21, and 22-32 years post-disturbance) the browse density was always largest 22-32 years post-disturbance regardless of path type (Table 2.2). In winter browse density at large feeding stations 1-11 years post-disturbance was 9.3 ± 2.6 twigs/m^2. The density nearly doubled to 18.4 ± 2.2 twigs/m^2 12-21 years post-disturbance and then increased to 20.2 ± 5.04 twigs/m^2 22-32 years post-disturbance (Table 2.2). The difference in density between the three age classes at large feeding station paths and random feeding station paths was not significantly different between the three age classes (ANOVA, $F_{2, 27} < 3.2$, $P > 0.06$) while the differences at random plot paths and straight transects were significant (ANOVA, $F_{2, 27} > 3.48$, $P < 0.045$).

In contrast to winter density, summer browse density decreased with stand age, although the relationship was again weak ($R^2 < 0.27$; Fig 2.3). When summer browse density was averaged in three age classes the browse density was always largest 1-11 years post-disturbance regardless of path type. Density at regenerating stands measured by large feeding stations was 12.7 ± 3.4 twigs/m^2. The density decreased to 7.1 ± 1.1 twigs/m^2 12-21 years post-disturbance, and then decreased to 5.3 ± 1.2 twigs/m^2 22-32 years post-disturbance (Table 2.2). The difference between age classes was significant

when measured by large feeding station paths (ANOVA, $F_{2, 25} = 4.5$, $P = 0.02$). However, the difference in browse density among the three age classes was not significant when measured by random feeding station paths, random plot paths, and straight transects (ANOVA, $F_{2, 25} < 3.4$, $P > 0.051$). Large feeding station paths again had the highest density, followed by random feeding station paths, random plot paths, and then straight transects in both winter and summer (Table 2.2).

Available Species Composition

Winter

In winter 75% of the available twigs along foraging paths were hazel, paper birch, willow, and balsam fir (Table 2.3). At these locations there was no significant difference in the available species composition measured by the four path types (Kruskal-Wallis test, $H_3 < 6.69$, $P > 0.08$). Similarly, within regenerating stands 75% of the available twigs were again hazel, paper birch, and balsam fir plus mountain maple and again, there was no significant difference in the available species composition measured by the four path types in winter at regenerating stands (Kruskal-Wallis test, $H_3 < 3.15$, $P > 0.37$; Table 2.3).

Most (34 of 44) species composition comparisons between foraging paths and regenerating stands measured by each path type in winter were not significantly different (Kruskal-Wallis test, $H_3 < 3.65$, $P > 0.06$). However, there was a significant difference between the available proportion along foraging paths and within regenerating stands for balsam fir measured by large feeding station paths, mountain maple measured by large feeding stations paths, paper birch measured by large feeding station paths, random feeding station paths, and random plot paths, and quaking aspen measured by large

feeding station paths, random plot paths and straight transects (Kruskal-Wallis test, $H_3 > 2.8$, $P < 0.05$; Table 2.3).

Summer

In summer 75% of the available twigs at foraging paths were mountain maple, willow, hazel, and quaking aspen (Table 2.4). There was no significant difference in the available species composition measured by the four path types at summer foraging paths (Kruskal-Wallis test, $H_3 < 6.75$, $P > 0.08$). At regenerating stands in summer 70% of the available twigs were again mountain maple, willow, and hazel with the addition of juneberry (Table 2.4). As in the foraging paths, within the regenerating stands in summer there was no significant difference in the available species composition measured by the four path types (Kruskal-Wallis test, $H_3 < 3.15$, $P > 0.37$). The one exception occurred in both foraging paths and regenerating stands when approximately 38% of available twigs were hazel along straight transects while 14% were hazel at large feeding stations (Kruskal-Wallis test, $H_3 > 9.69$, $P < 0.02$).

Most (36 of 44) species composition comparisons between foraging paths and regenerating stands by each path type in summer were not significantly different (Kruskal-Wallis test, $H_3 < 3.58$, $P > 0.06$). However, there was a significant difference between the available proportion at foraging paths and regenerating stands for juneberry measured by all path types, red-osier dogwood measured by random plot paths and straight transects, mountain ash measured by random feeding station paths and random plot paths, and rarely available species measured by large feeding station paths, random feeding station paths, and random plot paths (Kruskal-Wallis test, $H_3 > 4.47$, $P < 0.03$; Table 2.4).

Regenerating Stand Age

Species composition at the regenerating stands varied by age class. Most of the changes between age classes were true in winter and summer. Paper birch, quaking aspen and pin cherry were most abundant 1-11 years post-disturbance and became less available with increasing stand age in both seasons (Tables 2.5 and 2.6). Hazel, mountain maple, and juneberry were available in low proportions 1-11 years post-disturbance and became increasingly available with stand age in both seasons. Hazel and mountain maple became common enough to be two of the top four available species by 22 years post-disturbance. Balsam fir was only measured in winter, but it was also found in low proportions at young stands and became increasingly available 12 years post-disturbance. Red-osier dogwood and red maple consistently occurred at low proportions in all age classes in both seasons. Mountain ash was also available at consistently low proportions in all age classes in summer and was included in the "rarely available" species in winter.

Willow was the only species with different trends depending on the season. In winter, willow was most abundant 1-11 years post-disturbance and became less available in older stands (Table 2.5). In summer willow occurred at similar proportions in all three age classes (Table 2.6). However, the average amount of willow was skewed toward a higher estimate at the 12-21 year and 22-32 year post-disturbance regenerating stands because a few sites in each of these age classes had more than 50% willow while most of the sites in those age classes had 0% willow.

Many (22 of 44) species composition comparisons between age classes were not significantly different (Kruskal-Wallis test, $H_3 < 5.43$, $P > 0.07$). However, there was a significant difference between the available proportion at the three age classes for hazel

and mountain maple measured by all path types, paper birch measured by all paths except random feeding station paths, quaking aspen and willow measured by straight transects, balsam fir measured by large feeding station paths and straight transects, and red maple measured by all paths except large feeding station paths (Kruskal-Wallis test, $H_3 > 8.10$, $P < 0.04$; Table 2.5).

Most (37 of 44) species composition comparisons between age class in summer were not significantly different (Kruskal-Wallis test, $H_3 < 7.55$, $P > 0.06$). However, there was a significant difference between the available proportion at the three age classes for paper birch measured by large feeding station paths and random plot paths, quaking aspen measured by large feeding station paths and straight transects, pin cherry measured by large feeding station paths, red maple measured by random feeding station paths and random plot paths, and rarely available species measured by random feeding station paths (Kruskal-Wallis test, $H_3 > 8.10$, $P < 0.04$; Table 2.6).

Within each age class the proportions of each species measured by the four path types were never statistically different in winter (Kruskal-Wallis test, $H_3 < 4.56$, $P > 0.20$) or summer (Kruskal-Wallis test, $H_3 < 6.97$, $P > 0.07$).

Foraging Path Stand Age

In winter 8 of 29 foraging paths were in stands 1-11 years post-disturbance, 11 were in stands 12-21 years post-disturbance, none were in stands 22-32 years post-disturbance and the remaining 10 were in stands 33+ years post-disturbance. In summer 2 of 42 foraging paths were in regenerating stands 1-11 years post-disturbance, 10 were in stands 12-21 years post-disturbance, 3 were in stands 22-32 years post-disturbance and the remaining 27 were in stands 33+ years post-disturbance.

Because over two thirds of the foraging paths in summer were in stands 33+ years post-disturbance we averaged the available species composition at the foraging paths we measured in that age class. At these foraging paths 55% of the available twigs at large feeding stations were mountain maple, 15% were hazel, 8% were quaking aspen, and 7% were willow (Table 2.7).

Discussion

Browse species composition was similar at foraging paths and regenerating stands. This led us to reject our first hypothesis that foraging paths would have more commonly browsed species available than the regenerating stands. It also indicates that some regenerating stands have a species composition that is similar to areas in which moose are choosing to forage. This provides evidence that moose habitat restoration projects which create regenerating forest by harvesting, shearing, or otherwise removing older plant growth can effectively provide the same browse species in similar proportions to current foraging locations.

The distance moose traveled to complete ten large feeding stations along a foraging path (and the distance we traveled to complete ten simulated large feeding stations within regenerating stands) was half of the distance required to complete ten plots of the other three path types in summer and one quarter the distance in winter. This indicates that browsing moose would reduce travel time between feeding stations while gaining the greatest amount of browse.

Browse density along foraging paths and within regenerating stands was not significantly different in summer and in most comparisons in winter. The few that were statistically different in winter were not biologically different. For example, the density

at foraging paths estimated by biomass along random feeding stations in winter (1.7 ± 0.1 g/m^2) was 0.7 g/m^2 smaller than at regenerating stands (2.4 ± 0.2 g/m^2). This led us to reject our second hypothesis that moose were foraging in areas with higher browse densities than recently disturbed areas that we selected at random. This also provides support for moose habitat restoration projects because regenerating stands provide a similar density of twigs as areas which moose are foraging in based on GPS collar locations.

We partially accepted our third hypothesis that browse density would be highest in young stands and decrease with age because we observed this trend in summer but not in winter. Browse density is widely accepted to decrease with stand age (Peek 1997) although the winter trend we measured was also observed in Alaska (Weixelman et al. 1998). Part of the winter browse density trend was due to counting balsam fir and hazel as available species in winter but not in summer. Balsam fir and hazel have growth patterns that increase the number of these plants in a stand and the number of twigs per plant (Ward and Moen in review). These characteristics allowed very high twig counts of hazel and balsam fir in short distances in winter. However, hazel and balsam fir did not become prevalent in the regenerating stands we measured until 12 years post-disturbance in winter, which is also when winter densities began to increase above 20 twigs/m^2 (Fig. 2.3). By 22 years post-disturbance hazel and balsam fir made up >65% of the available twigs we measured. Therefore, because hazel and balsam fir had high twig counts when present, and they became more prevalent as stands aged, the overall browse density increased as stands aged in winter.

We were surprised that hazel was present in low proportions in stands 1-11 years post-disturbance in winter because it is one of the most constant species across the landscape and was abundant in summer stands we measured 1-11 years post-disturbance. One explanation for this discrepancy was that we only measured six stands in the youngest age class in winter. It is possible that increasing the number of plots sampled would modify the proportion of hazel in younger stands.

Browse density was significantly different among path types and large feeding stations always had higher densities of browse. Browse density from the perspective of a moose that forages from large feeding station to large feeding station is greater than browse density that is measured with a straight transect. Similarly, using the large feeding station method to measure available browse would result in measuring browse patches with high densities of twigs. Browse density measured at what we call large feeding stations will be greater than browse densities measured by straight transects or square quadrats. Additionally, browse species composition was similar regardless of the path type in both randomly selected regenerating stands and actual moose foraging paths. This provides additional evidence for the accuracy of the large feeding station method.

The foraging paths we measured occurred evenly in three of four age classes in winter (1-11, 12-21, and 33+ years post-disturbance), but in summer the foraging paths were mostly in the 12-21 and 33+ years post-disturbance age classes. We never measured a foraging path in the 22-32 year age class in winter and only three of the summer foraging paths were in this age class indicating that stands in the age class may have a characteristic that deters moose from foraging in them. It is also possible that when we chose which foraging paths to measure these 22-32 year old stands were less accessible

and therefore measured less often. However, since stands in this age class were harvested 22-32 years earlier, there are often roads or paths leading to them, which indicates that lack of access may not have been a factor. A more likely explanation is that moose are choosing to walk through these 22-32 year old stands instead of stopping to browse. The stands between 22 and 32 years post-disturbance in winter have >65% hazel and balsam fir, and in summer (when balsam fir was not counted) hazel was 12% of the available twigs at large feeding stations and 43% of the available twigs at straight transects. Additionally, because hazel and balsam fir are so common they are consumed, but classified as avoided, in summer and winter (Ward and Moen in review). This indicates that stands between 22 and 32 years of age offer many twigs of two negatively selected species and small amounts of other species.

Although the browse density of summer twigs we measured was highest in the youngest age class, only two of the 42 foraging paths we measured were in the 1-11 year age class while two thirds of the foraging paths we measured were in stands 33+ years post-disturbance. One explanation for this is that our foraging paths were measured in mid to late summer when leaves in shaded areas are more nutritious and senesce later (Peek 1997, Augsburger and Bartlett 2003). Moose also appeared to prefer mature stands in late summer in Minnesota in the past (Peek et al. 1976). Moose could also be foraging in shaded areas because of other benefits such as cover from predators, cooler air temperatures, and closer proximity to thermal refugia.

Because our youngest age class had a small sample size and our study area was restricted to the southern edge of moose range in northeastern Minnesota we cannot make any statements about the best years post-disturbance for browse availability in

northeastern Minnesota with confidence. However we can suggest trends based on our data that should be tested. First, the data suggests that although stands 22-32 years post-disturbance in winter offered the highest densities of common browse species, we did not observe moose foraging in these stands. Second, although the youngest stands offered the highest browse densities and high quantities of three of the most common browse species in summer, we had only two moose foraging paths in this age class. These trends suggest that factors other than browse density and available browse species composition influence where moose forage. This data also indicates that moose use stands of different ages for foraging during late summer and winter. One possible future test would be to analyze the entire data set of locations for all GPS collared moose instead of focusing on only the foraging paths we visited (Ward and Moen, in review).

In efforts to restore moose habitat, maintaining a mosaic landscape of many different stand ages may help provide moose with different habitats and browse species. Future research should be completed across a larger area of moose range in Minnesota to determine which stand ages provide the best browse for moose in the region. Furthermore, measuring stands in the years following different disturbances such as fire, wind throw, and forest harvest could inform us about effects these various disturbances have on browse density and composition in Minnesota.

Table 1.1. The common and scientific names for each potential browse species in northeastern Minnesota and in which seasons they are consumed. “Rare” species were defined as those making up less than 1% of the diet at large feeding station paths. “Not Browsed” species were defined as those without a single bite consumed along our foraging paths.

Common Name	Scientific Name	Winter	Summer
Balsam fir	*Abies balsamea*	Common	Not Browsed
Red maple	*Acer rubrum*	Common	Common
Mountain maple	*Acer spicatum*	Common	Common
Alder	*Alnus rugosa*	Rare	Rare
Juneberry	*Amelanchier* spp.	Common	Common
Paper birch	*Betula papyrifera*	Common	Common
Bog birch	*Betula pumila*	Not Browsed	Rare
Red-osier dogwood	*Cornus stolonifera*	Common	Rare
Beaked hazel	*Corylus cornuta*	Common	Rare
Black ash	*Fraxinus niger*	Not Browsed	Rare
White pine	*Pinus strobus*	Rare	Rare
Balsam poplar	*Populus balsamifera*	Rare	Rare
Quaking aspen	*Populus tremuloides*	Common	Common
Pin cherry	*Prunus pennsylvanicus*	Common	Common
Choke cherry	*Prunus virginianus*	Common	Common
Oak	*Quercus* spp.	Not Browsed	Rare
Willow	*Salix* spp.	Common	Common
Elderberry	*Sambucus pubens*	Not Browsed	Rare
Mountain ash	*Sorbus decora*	Rare	Common

Table 1.2. Diameter-at-point-of-browsing–biomass regression equations on base-10 log transformed data, R^2, and N for all browse species in winter in open and closed canopy (y = dry mass, x = diameter-at-point-of-browsing). Open canopy indicates twigs grown in locations shaded 0-50% and closed canopy indicates twigs grown in locations shaded 70-100%.

Species	Canopy	N	Regression Equation	R^2
Balsam fir	Open	49	y = -0.67 + 2.04x	0.69
	Closed	31	y = -0.51 + 1.76x	0.69
Red maple	Open	120	y = -1.53 + 2.47x	0.83
	Closed	90	y = -1.50 + 2.69x	0.88
Mountain maple	Open	165	y = -1.38 + 2.50x	0.71
	Closed	166	y = -1.10 + 1.92x	0.62
Juneberry	Open	184	y = -0.95 + 1.73x	0.63
	Closed	47	y = -1.01 + 2.20x	0.88
Paper birch	Open	142	y = -1.08 + 2.25x	0.73
	Closed	52	y = -1.08 + 2.25x	0.84
Hazel	Open	197	y = -0.87 + 1.52x	0.50
	Closed	138	y = -0.75 + 1.09x	0.39
Red-osier dogwood	Open	121	y = -1.47 + 2.80x	0.72
	Closed	110	y = -1.28 + 2.27x	0.72
Quaking aspen	Open	173	y = -0.73 + 1.23x	0.43
	Closed	27	y = -1.10 + 1.92x	0.72
Pin cherry	Open	175	y = -1.05 + 1.83x	0.54
	Closed	22	y = -1.15 + 2.17x	0.88
Choke cherry	Open	106	y = -0.69 + 1.16x	0.66
	Closed	41	y = -0.66 + 0.58x	0.16
Willow	Open	175	y = -1.35 + 2.66x	0.81
	Closed	11	y = -1.13 + 2.36x	0.90
Mountain ash	Open	84	y = -0.90 + 1.58x	0.47
	Closed	164	y = -1.43 + 2.22x	0.69

Table 1.3. Diameter-at-point-of-browsing–biomass regression equations on base-10 log transformed data, R^2, and N for all browse species in summer in open and closed canopy (y = dry mass, x = diameter-at-point-of-browsing). Open canopy indicates twigs grown in locations shaded 0-50% and closed canopy indicates twigs grown in locations shaded 70-100%.

Species	Canopy	N	Regression Equation	R^2
Red maple	Open	63	y = -0.52 + 1.54x	0.64
	Closed	59	y = -0.50 + 1.48x	0.51
Mountain maple	Open	124	y = -0.79 + 1.72x	0.61
	Closed	67	y = -0.82 + 1.69x	0.41
Juneberry	Open	124	y = -0.47 + 0.84x	0.16
	Closed	12	y = -0.47 + 1.46x	0.79
Paper birch	Open	160	y = -0.47 + 1.02x	0.33
	Closed	76	y = -0.53 + 0.89x	0.24
Hazel	Open	248	y = -0.34 + 0.85x	0.25
	Closed	105	y = -0.50 + 1.36x	0.44
Red-osier dogwood	Open	216	y = -0.39 + 1.08x	0.59
	Closed	34	y = -0.33 + 0.45x	0.08
Quaking aspen	Open	112	y = -0.51 + 1.34x	0.64
	Closed	19	y = -0.80 + 1.64x	0.68
Pin cherry	Open	92	y = -0.50 + 1.15x	0.39
	Closed[1]	0	NA	NA
Choke cherry	Open	64	y = -0.26 + 0.45x	0.11
	Closed	109	y = -0.62 + 1.70x	0.69
Willow	Open	96	y = -0.80 + 2.07x	0.64
	Closed	66	y = -0.62 + 1.23x	0.73
Mountain ash	Open	146	y = -0.45 + 0.83x	0.14
	Closed	48	y = -0.74 + 1.69x	0.77

[1]We never found any unbrowsed pin cherry in closed canopy.

Table 1.4. Summary statistics on browsed twigs of all browse species in winter. Open canopy indicates twigs grown in locations shaded 0-50% and closed canopy indicates twigs grown in locations shaded 70-100%. P-values indicate *t*-test results between the diameter-at-point-of-browsing (DPB) of each species in open and closed canopy.

		Diameter at Point of Browsing (mm)					
Species	Canopy	Mean ± SE	Minimum	Maximum	Mean Bite ± SE (g)	N	*P*
Balsam fir**	Open	2.7 ± 0.1	0.9	6.5	1.6 ± 0.3	82	*0.002*
	Closed	2.2 ± 0.1	1.0	4.0	1.2 ± 0.2	50	
Red maple**	Open	3.5 ± 0.1	1.3	7.4	0.7 ± 0.3	125	*0.009*
	Closed	4.1 ± 0.1	2.7	6.9	1.4 ± 0.5	27	
Mountain maple*	Open	2.8 ± 0.3	1.5	4.6	0.6 ± 0.3	47	*0.019*
	Closed	2.4 ± 0.3	0.4	4.9	0.4 ± 0.2	56	
Juneberry	Open	2.4 ± 0.1	0.9	4.5	0.5 ± 0.1	161	*0.583*
	Closed[1]	NA	NA	NA	NA	8	
Paper birch	Open	2.7 ± 0.1	0.6	4.8	0.8 ± 0.1	188	*NA*
	Closed[1]	NA	NA	NA	NA	7	
Hazel	Open	2.7 ± 0.1	1.1	5.3	0.6 ± 0.1	301	*0.104*
	Closed	2.8 ± 0.1	1.1	4.5	0.6 ± 0.1	132	
Red-osier dogwood***	Open	3.5 ± 0.1	1.5	6.1	1.1 ± 0.1	332	*<0.0001*
	Closed	4.3 ± 0.2	2.0	6.6	1.4 ± 0.4	40	
Quaking aspen	Open	3.5 ± 0.1	0.9	6.8	0.9 ± 0.1	209	*0.155*
	Closed	3.2 ± 0.1	1.0	5.7	0.7 ± 0.4	32	
Pin cherry	Open	2.4 ± 0.1	0.6	4.9	0.4 ± 0.1	216	*NA*
	Closed[1]	NA	NA	NA	NA	6	

Table 1.4 continued on next page

Table 1.4 continued

Choke cherry	Open	3.0 ± 0.3	1.5	4.8	0.7 ± 0.1	53	*0.120*
	Closed	2.6 ± 0.4	0.2	4.1	0.4 ± 0.1	20	
Willow	Open	3.1 ± 0.1	0.5	6.4	0.9 ± 0.1	501	*NA*
	Closed[1]	NA	NA	NA	NA	0	
Mountain ash*	Open	4.3 ± 0.1	1.6	6.8	1.3 ± 0.3	43	*0.045*
	Closed	3.7 ± 0.1	1.2	8.4	0.7 ± 0.5	53	
Combined	Open	3.0 ± 0.02	0.5	9.0	NA	2388	
	Closed	3.1 ± 0.1	0.2	8.4	NA	454	

[1]We did not find enough individual twigs of juneberry, paper birch, pin cherry, or willow in closed canopy to calculate reliable means for those categories.

Table 1.5. Summary statistics on browsed twigs of all browse species in summer. Open canopy indicates twigs grown in locations shaded 0-50% and closed canopy indicates twigs grown in locations shaded 70-100%. P-values indicate *t*-test results between the diameter-at-point-of-browsing (DPB) of each species in open and closed canopy.

		Diameter at Point of Browsing (mm)					
Species	Canopy	Mean ± SE	Minimum	Maximum	Mean Bite ± SE (g)	N	*P*
Red maple	Open[1]	NA	NA	NA	NA	14	*0.349*
	Closed	2.8 ± 0.2	1.3	6.0	1.4 ± 0.3	27	
Mountain maple***	Open	2.3 ± 0.03	0.5	4.7	0.7 ± 0.1	675	*<0.0001*
	Closed	3.0 ± 0.1	0.5	4.9	1.0 ± 0.1	264	
Juneberry	Open	1.6 ± 0.04	0.1	3.2	0.5 ± 0.04	149	*0.145*
	Closed	2.1 ± 0.3	0.2	4.2	1.0 ± 0.4	20	
Paper birch**	Open	2.3 ± 0.1	0.02	5.1	0.8 ± 0.1	316	*0.003*
	Closed	2.0 ± 0.1	0.6	3.8	0.5 ± 0.1	84	
Hazel	Open	1.6 ± 0.1	0.5	3.5	0.7 ± 0.04	105	*0.739*
	Closed	1.6 ± 0.1	0.6	2.5	0.6 ± 0.1	48	
Red-osier dogwood***	Open	2.9 ± 0.1	1.5	5.7	1.3 ± 0.1	41	*0.001*
	Closed	2.1 ± 0.2	0.5	4.4	0.7 ± 0.1	26	
Quaking aspen***	Open	3.1 ± 0.2	0.5	11.1	1.4 ± 0.2	169	*<0.0001*
	Closed	1.6 ± 0.1	0.3	4.3	0.3 ± 0.2	53	
Pin cherry	Open	2.2 ± 0.1	0.6	4.2	0.8 ± 0.1	53	*NA*
	Closed[1]	NA	NA	NA	NA	0	

Table 1.5 continued on next page

Table 1.5 continued

Choke cherry	Open	2.2 ± 0.1	1.0	4.1	0.8 ± 0.1	44	*0.085*
	Closed	2.0 ± 0.1	0.8	3.9	0.8 ± 0.1	80	
Willow***	Open	2.3 ± 0.1	0.5	5.5	0.9 ± 0.1	242	*<0.0001*
	Closed[1]	NA	NA	NA	NA	14	
Mountain ash	Open	4.0 ± 0.1	2.0	7.0	1.1 ± 0.1	72	*0.802*
	Closed[1]	NA	NA	NA	NA	7	
All Species	Open	2.3 ± 0.02	0.02	11.1	NA	2071	*NA*
	Closed	2.4 ± 0.04	0.2	6.1	NA	627	

[1]We did not find enough individual twigs of red maple in open canopy or pin cherry, willow, or mountain ash in closed canopy to calculate reliable means for those categories.

Table 1.6. Available browse density and consumed browse density along the distance of the four path types in summer and winter measured by twigs/m^2 ± SE and biomass (g)/m^2 ± SE. W = winter, S = summer.

	Method	Season	Large Feeding Station	Random Feeding Station	Random Plot	Straight Transect
Available	# Twigs	W	15.4 ± 1.6	2.3 ± 0.2	2.0 ± 0.2	1.4 ± 0.2
		S	5.9 ± 0.6	2.0 ± 0.2	1.8 ± 0.3	1.1 ± 0.1
	Biomass	W	9.9 ± 1.0	1.7 ± 0.1	1.5 ± 0.1	1.0 ± 0.1
		S	15.2 ± 1.7	6.8 ± 1.9	4.5 ± 0.8	2.9 ± 0.4
Consumed	# Twigs	W	5.3 ± 0.6	2.1 ± 0.1	0.5 ± 0.1	0.2 ± 0.03
		S	2.7 ± 0.3	1.0 ± 0.3	0.4 ± 0.1	0.1 ± 0.03
	Biomass	W	4.0 ± 0.4	0.5 ± 0.04	0.4 ± 0.04	0.2 ± 0.02
		S	6.7 ± 0.7	2.4 ± 0.4	1.0 ± 0.2	0.3 ± 0.04

Table 1.7. Percent of available twigs consumed at the four path types in winter and summer.

		Percent of Available Twigs Consumed			
Season	N	Large Feeding Station	Random Feeding Station	Random Plot	Straight Transect
Winter	29	35 ± 2	27 ± 2	23 ± 2	13 ± 3
Summer	31	45 ± 2	35 ± 3	25 ± 2	9 ± 2

Table 1.8. Diet composition (mean percent of diet ± SE) measured by four path types in winter 2013. Means and SE were weighted by moose. Rare includes species that made up <1% of the diet at large feeding station paths. N is the number of foraging paths measured.

Species	Large Feeding Station	Random Feeding Station	Random Plot	Straight Transect
Hazel	27 ± 7	26 ± 8	27 ± 9	28 ± 8
Paper birch	26 ± 7	26 ± 6	25 ± 6	18 ± 6
Willow	11 ± 5	14 ± 6	13 ± 6	11 ± 5
Quaking aspen	7 ± 3	8 ± 4	10 ± 5	13 ± 6
Juneberry	6 ± 2	5 ± 2	4 ± 1	4 ± 2
Red maple	5 ± 3	4 ± 2	5 ± 3	4 ± 4
Red-osier dogwood	5 ± 4	3 ± 3	3 ± 3	10 ± 11
Balsam fir	4 ± 2	6 ± 2	6 ± 3	2 ± 2
Mountain maple	4 ± 3	3 ± 1	2 ± 1	2 ± 1
Cherry	3 ± 1	2 ± 1	2 ± 1	2 ± 1
Rare	2 ± 2	2 ± 1	2 ± 1	5 ± 6
N	29	29	29	29

Table 1.9. Diet composition (mean percent of diet ± SE) measured by four path types in summer 2012. Means and SE were weighted by moose. Rare includes all species that made up <1% of the diet at large feeding station paths. N is the number of foraging paths measured.

Species	Large Feeding Station	Random Feeding Station	Random Plot	Straight Transect
Mountain maple	42 ± 11	45 ± 10	43 ± 11	25 ± 11
Willow	21 ± 8	21 ± 9	28 ± 11	23 ± 11
Paper birch	11 ± 3	9 ± 4	6 ± 4	6 ± 5
Cherry	9 ± 4	7 ± 4	6 ± 4	3 ± 5
Quaking aspen	8 ± 4	10 ± 3	8 ± 3	14 ± 7
Mountain ash	4 ± 2	3 ± 2	4 ± 4	0
Juneberry	2 ± 1	3 ± 2	2 ± 1	8 ± 5
Red maple	1 ± 1	0	0	7 ± 4
Rare	1 ± 0.3	1 ± 0.4	0.2 ± 0.1	10 ± 7
N	31	31	31	31

Table 1.10. Diet composition of individual moose in winter 2013 measured by twigs consumed at large feeding station paths. There are diets for eight collared moose and one diet for all of the foraging paths of uncollared moose in the Greenwood Lake (GW Lake) area. 31189 and 31190 are male, the rest are females. N is the number of foraging paths measured. Rare species are those that made up <1% of the combined moose diet at large feeding stations.

		Moose Number								
Species	All Moose	31166	31174	31175	31178	31180	31182	31189	31190	GW Lake
Hazel	27	21	38	29	13	50	33	9	68	8
Paper birch	26	14	41	15	57	9	3	56	3	20
Willow	11	5			9	6		5	3	46
Quaking aspen	7	28		16	12	<1	8	2		7
Juneberry	6	18			1	8		9	1	13
Red maple	5					26		9		
Red-osier dogwood	5			15		<1	38	4		
Balsam fir	4	2	4	15	1		14			5
Mountain maple	4		16		1			1	25	
Cherry	3	11	1	5	6	<1	3	6		
Rare	1	2		5		1				
N	29	2	2	3	3	4	2	5	3	5

Table 1.11. Diet composition of individual moose in summer 2012 measured by twigs consumed at large feeding station paths. There are diets for seven collared moose and one diet for the foraging paths of uncollared moose in the Greenwood Lake (GW Lake) area and one diet for the foraging paths of uncollared moose in the Wilson Lake area. 31189 and 31190 are male, the rest are females. N is the number of sites measured. Rare species are those that made up <1% of the combined moose diet at large feeding stations.

		Moose Number								
Species	All Moose	31166	31168	31175	31178	31180	31189	31190	GW Lake	Wilson Lake
Mountain maple	41	3	57	84	90	36	57	10	39	17
Willow	21	53	3	9		17		61	55	10
Paper birch	11	12			1	17	13	7		29
Cherry	9	8	5	3	2	24	1	3		31
Quaking aspen	8	4	36			1	23	2	2	2
Mountain ash	4	17			5	5		3		6
Juneberry	2						1	12		3
Red maple	1						5			
Rare	1			1	1			3	4	
N	31	3	2	3	3	3	6	4	2	5

Table 1.12. Browse species selection in both seasons when data from all moose was combined. If the moose were simply browsing at random, we would expect the 95% confidence interval of the percent browsed to contain the percent available at large feeding stations.

Season	Species	Percent Available at Large Feeding Stations	95% Confidence Interval of Percent Browsed at Large Feeding Stations	Selection
Winter	Juneberry	4.7	5.1 ≤ - ≥ 6.8	+
	Red maple	3.3	3.8 ≤ - ≥ 5.3	+
	Mountain maple	2.7	4.0 ≤ - ≥ 5.5	+
	Paper birch	19.3	24.7 ≤ - ≥ 27.9	+
	Red-osier dogwood	2.1	3.3 ≤ - ≥ 4.8	+
	Quaking aspen	5.6	5.8 ≤ - ≥ 7.6	+
	Cherry	3.0	2.7 ≤ - ≥ 4.0	0
	Willow	11.9	11.2 ≤ - ≥ 13.5	0
	Balsam fir	9.0	2.8 ≤ - ≥ 4.1	-
	Hazel	36.8	26.3 ≤ - ≥ 29.5	-
Summer	Red maple	0.5	0.6 ≤ - ≥ 1.3	+
	Mountain maple	27.6	34.6 ≤ - ≥ 38.2	+
	Cherry	7.2	8.3 ≤ - ≥ 10.5	+
	Mountain ash	4.2	8.6 ≤ - ≥ 10.8	+
	Juneberry	3.3	2.2 ≤ - ≥ 3.4	0
	Paper birch	10.4	9.8 ≤ - ≥ 12.1	0
	Quaking aspen	8.1	6.1 ≤ - ≥ 8.1	0
	Willow	28.6	18.9 ≤ - ≥ 21.9	-

Table 1.13. Comparison of winter diet composition in NE MN estimated by our large feeding stations and by previous research (Peek et al.1976). In this ranking system 1 = most important browse species based on percent of diet.

Season	Species	This Study %	Peek et al. (1976) %	This Study Rank	Peek et al. (1976) Rank
Winter	Hazel	27	20	1	2
	Paper birch	26	8	2	6
	Willow	11	21	3	1
	Quaking aspen	7	11	4	4
	Juneberry	6	5	5	8
	Red maple	5	0	6	
	Red-osier dogwood	5	8	7	5
	Balsam fir	4	11	8	3
	Mountain maple	4	5	9	7
	Cherry[1]	3	3	10	10
	Mountain ash	<1	4		9
Summer	Mountain maple	41	6	1	5
	Willow	21	26	2	2
	Paper birch	11	12	3	3
	Cherry[1]	9	11	4	4
	Quaking aspen	8	32	5	1
	Mountain ash	4	3	6	6
	Juneberry	2	2	7	8
	Red maple	1	<1	8	
	Red-osier dogwood	<1	2	9	7
	Hazel	<1	<1	10	9

[1] Peek et al. (1976) only measured pin cherry and this study combined pin cherry and choke cherry in this calculation.

Table 2.1. The available density of twigs and biomass along foraging paths and within regenerating stands in winter and summer. *P* values are from *t*-tests comparing twig density (or biomass density) in foraging paths to twig density (or biomass density) in regenerating stands. All comparisons of browse density among path types in each site were significantly different (ANOVA, Foraging Paths Winter $F_{3, 112} > 66.1$; Regenerating Stands Winter $F_{3, 116} > 40.9$; Foraging Paths Summer $F_{3, 164} > 14.8$, Regenerating Stands Summer $F_{3, 116} > 36.3$; all $p < 0.0001$). FS = Feeding Station.

		Mean Available Density					
		Twigs/m^2			Biomass/m^2		
Season	Path Type	Foraging Paths	Regenerating Stands	*P*	Foraging Paths	Regenerating Stands	*P*
Winter	Large FS	15.4 ± 1.6	17.8 ± 2.3	*0.51*	9.9 ± 1.0	14.0 ± 1.7	*0.08*
	Random FS	2.6 ± 0.1	2.9 ± 0.2	*0.44*	1.7 ± 0.1	2.4 ± 0.2	*0.01*
	Random Plot	2.3 ± 0.2	2.6 ± 0.2	*0.27*	1.5 ± 0.1	2.2 ± 0.2	*0.003*
	Straight Transect	1.7 ± 0.2	2.2 ± 0.2	*0.07*	1.0 ± 0.1	1.9 ± 0.2	*0.001*
Summer	Large FS	7.2 ± 1.2	7.0 ± 0.9	*0.91*	18.1 ± 3.2	16.7 ± 1.9	*0.75*
	Random FS	2.2 ± 0.2	2.0 ± 0.2	*0.42*	6.7 ± 1.4	4.8 ± 0.4	*0.25*
	Random Plot	2.0 ± 0.3	1.7 ± 0.2	*0.38*	4.7 ± 0.6	4.0 ± 0.4	*0.44*
	Straight Transect	1.3 ± 0.1	1.2 ± 0.1	*0.72*	3.1 ± 0.3	2.9 ± 0.3	*0.57*

Table 2.2. Browse density ± SE (twigs/m^2) in regenerating stands of three age classes measured by four path types in winter and summer. FS = Feeding Station. In winter N was 6 in the 1-11 years class and 12 in the 12-21 and 22-32 years classes. In summer N was 4 in the 1-11 years class, 12 in the 12-32 years class, and 11 in the 22-32 years class.

		Stand Age (years)			
Season	Path Type	1-11	12-21	22-32	*P*
Winter	Large FS	9.3 ± 2.6	18.4 ± 2.2	20.2 ± 5.0	*0.21*
	Random FS	2.0 ± 0.4	3.0 ± 0.2	3.1 ± 0.3	*0.06*
	Random Plot	1.7 ± 0.4	2.8 ± 0.2	2.7 ± 0.2	*0.03*
	Straight Transect	1.2 ± 0.4	2.5 ± 0.3	2.3 ± 0.3	*0.045*
Summer	Large FS	12.7 ± 3.4	7.1 ± 1.1	5.3 ± 1.2	*0.02*
	Random FS	2.5 ± 0.2	2.3 ± 0.3	2.0 ± 0.4	*0.051*
	Random Plot	2.0 ± 0.3	1.8 ± 0.2	1.5 ± 0.2	*0.16*
	Straight Transect	1.7 ± 0.3	1.3 ± 0.3	1.0 ± 0.2	*0.29*

Table 2.3. Mean available species composition (%) at all four path types along foraging paths (FP) and within regenerating stands (RS) in winter. Regenerating stands were chosen independently of moose foraging. Significant differences between foraging paths and regenerating stands at each path type are denoted by an asterisk. Sums do not add up to 100% because rare species are not shown. FS = Feeding Station.

	Path Type											
	Large FS			Random FS			Random Plot			Straight Transect		
Species	FP		RS	FP		RS	FP		RS	FP		RS
Hazel	34		32	32		34	34		34	39		30
Paper birch	20	*	12	19	*	13	17	*	13	10		12
Willow	11		8	12		6	11		6	8		5
Balsam fir	10	*	22	13	*	26	15	*	26	18		29
Quaking aspen	5	*	4	7		3	7	*	2	8	*	4
Juneberry	5		3	3		3	3		3	3		3
Red maple	4		<1	2		<1	2		<1	1		<1
Red-osier dogwood	3		3	2		2	2		2	3		2
Mountain maple	3	*	11	3		9	3		9	4		9
Pin cherry	3		2	2		3	3		3	2		2
Sum	98		97	97		96	98		98	98		96

Table 2.4. Mean available species composition at all four path types along foraging paths (FP) and within regenerating stands (RS) in summer. Regenerating stands were chosen independently of moose foraging. Significant differences between foraging paths and regenerating stands at each path type are denoted by an asterisk. Sums do not add up to 100% because rare species are not shown. FS = Feeding Station.

	Path Type											
	Large FS			Random FS			Random Plot			Straight Transect		
Species	FP		RS	FP		RS	FP		RS	FP		RS
Mountain maple	38		22	36		23	29		22	17		15
Willow	16		16	13		10	14		10	12		10
Hazel[1]	14		14	17		19	27		23	39		37
Quaking aspen	9		3	9		5	9		6	7		6
Paper birch	8		15	9		18	6		17	10		9
Mountain ash	3		1	4	*	1	4	*	0	2		1
Juneberry	3	*	17	3	*	13	3	*	10	4	*	7
Pin cherry	2		0	1		2	1		2	2		1
Red maple	1		6	1		5	1		5	2		6
Red-osier dogwood[1]	1		4	1		4	0	*	4	1	*	4
Sum	94		94	94		95	98		98	98		96

[1] These species are rare in the diet in summer (Ward and Moen in review)

Table 2.5. Available species composition at regenerating stands of three different age classes measured by four path types in winter. "LG FS" = Large Feeding Station path, "Rdm FS" = Random Feeding Station path, "Rdm Plot" = Random Plot path, "Strt Trans" = Straight Transect. Significant differences between age classes within one path type are denoted by an asterisk in the 1-11 years age class. There were no significant differences between the path types within an age class.

	Stand Age (years)											
	1-11				12-21				22-32			
Species	LG FS	Rdm FS	Rdm Plot	Strt Trans	LG FS	Rdm FS	Rdm Plot	Strt Trans	LG FS	Rdm FS	Rdm Plot	Strt Trans
Paper birch	43*	40	41*	43*	6	9	9	7	1	4	4	2
Willow	26	22	20	20*	7	2	1	2	1	3	3	1
Quaking aspen	18	10	10	18*	0	1	1	2	0	0	0	0
Pin cherry	8	8	7	1	1	3	3	5	1	1	1	0
Balsam fir	2*	12	13	2*	20	30	30	31	34	29	29	42
Red-osier dogwood	1	3	5	5	3	2	2	0	4	0	0	1
Hazel	0*	4*	4*	6*	45	39	39	38	35	44	44	34
Mountain maple	0*	0*	0*	0*	11	7	7	8	17	15	15	15
Juneberry	0	0	0	0	4	4	4	3	4	3	3	4
Red maple	0	0*	0*	0*	0	2	2	1	0	0	0	0
Sum	98	100	100	95	98	97	97	96	99	99	99	98
N	6				12				12			

Table 2.6. Available species composition at regenerating stands of three different age classes measured by four path types in summer. "LG FS" = Large Feeding Station path, "Rdm FS" = Random Feeding Station path, "Rdm Plot" = Random Plot path, "Strt Trans" = Straight Transect. Significant differences between age classes within one path type are denoted by an asterisk in the 1-11 years age class. There were no significant differences between the path types within an age class.

	Regenerating Stands (years)											
	1-11				12-21				22-32			
Species	LG FS	Rdm FS	Rdm Plot	Strt Trans	LG FS	Rdm FS	Rdm Plot	Strt Trans	LG FS	Rdm FS	Rdm Plot	Strt Trans
Paper birch	52*	40	38*	18	14	15	15	11	4	16	14	6
Quaking aspen	11*	16	21	29*	2	6	6	5	0	2	1	0
Willow	11	10	10	14	13	10	8	5	22	11	13	14
Juneberry	6	5	5	8	15	14	9	6	19	14	12	6
Hazel	6	14	15	18	18	20	24	38	12	19	24	43
Red-osier dogwood	5	1	1	1	3	4	5	7	5	5	4	2
Red maple	4	5*	2*	4	2	1	1	4	6	2	3	5
Pin cherry	2*	4	4	5	0	3	3	0	0	0	0	1
Mountain maple	1	2	2	1	28	24	23	15	22	31	28	20
Mountain ash	1	1	1	0	1	1	0	1	1	0	0	1
Sum	100	99	99	97	96	97	95	92	91	100	100	99
N	4				12				11			

Table 2.7. The percent of available twigs of each species at 27 foraging paths in the 33+ years post-disturbance age class in summer. FS = Feeding Station.

	Path Type			
Species	Large FS	Random FS	Random Plot	Straight Transect
Willow	7	12	13	8
Hazel	15	19	28	42
Mountain maple	55	43	34	15
Paper birch	5	5	3	11
Juneberry	1	2	2	5
Mountain ash	3	1	3	1
Red-osier dogwood	1	1	0	1
Quaking aspen	8	10	10	9
Pin cherry	0	0	0	2
Red maple	1	1	1	2
Rare	5	6	5	4

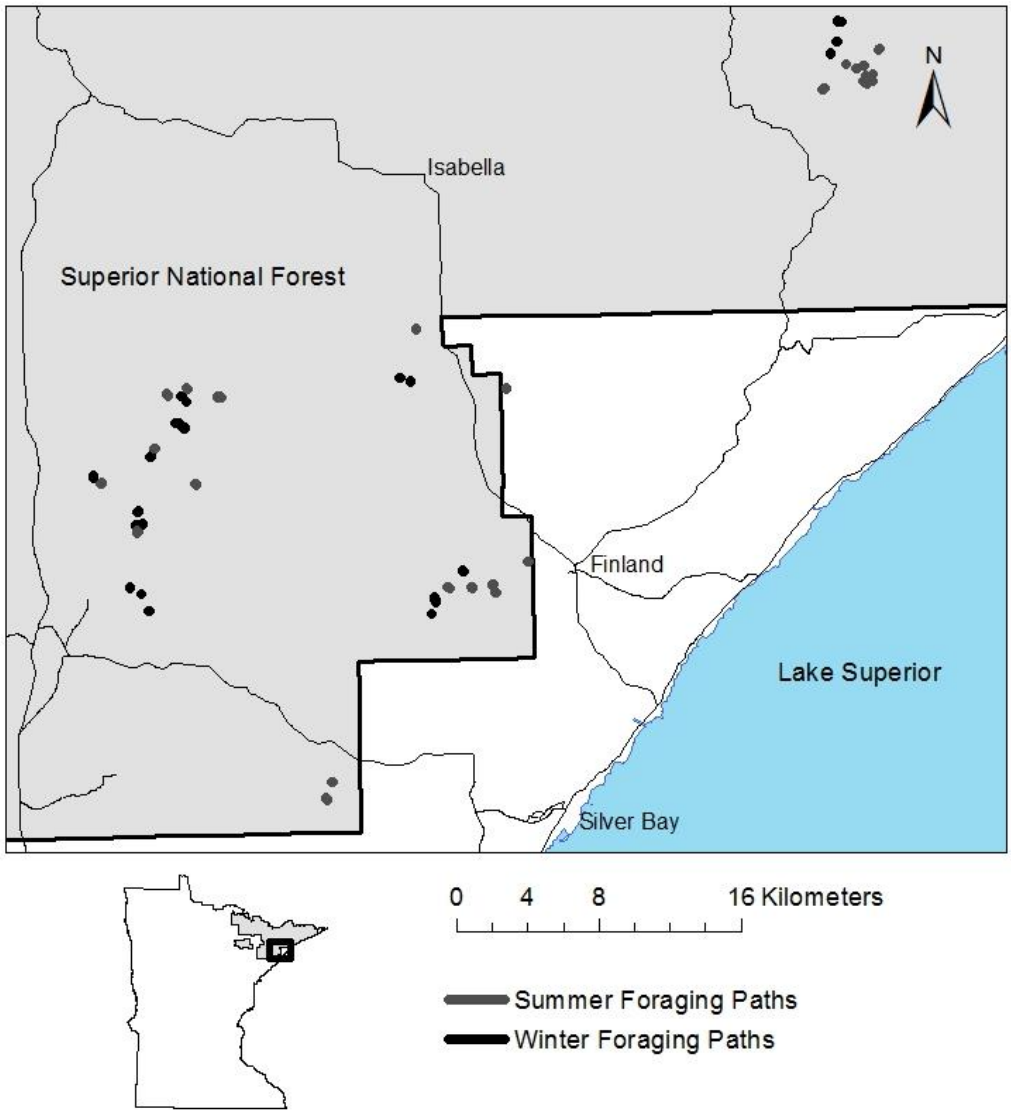

Fig. 1.1. The study area and locations of foraging paths in the Superior National Forest in northeastern Minnesota. Each black dot represents one measured foraging path in winter and a dark gray dot represents a summer foraging path.

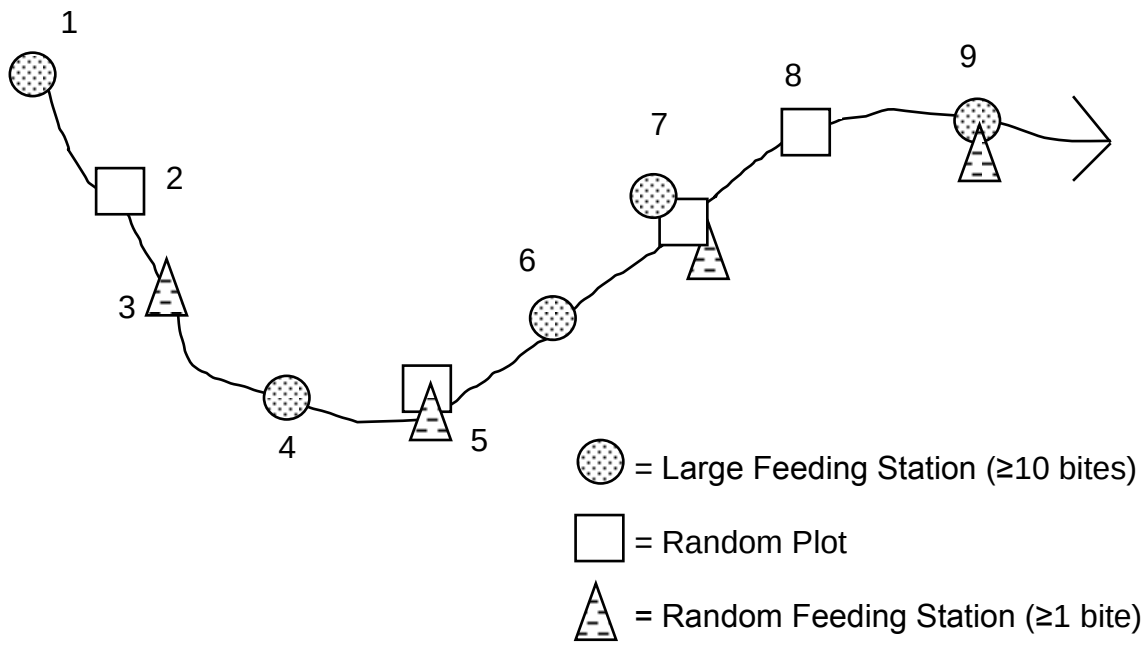

Fig. 1.2. A diagram of how we measured a foraging path with three path types. Plot 1 is a large feeding station (≥10 bites). Plot 2 is a random plot. Because Plot 2 does not have any bites taken we stop at the next bite which becomes Plot 3, a random feeding station. Plot 4 is the second large feeding station. Plot 5 is the second random plot with 1-9 bites, so it is also the second random feeding station. Plot 6 is the third large feeding station. Plot 7 is the third random plot that has ≥10 bites, so it is also the third random feeding station and the fourth large feeding station. Plot 8 is the fourth random plot. Plot 9 is the fourth random feeding station and has ≥10 bites, so it is also the fifth large feeding station. We would continue until we measured 10 plots of each path type.

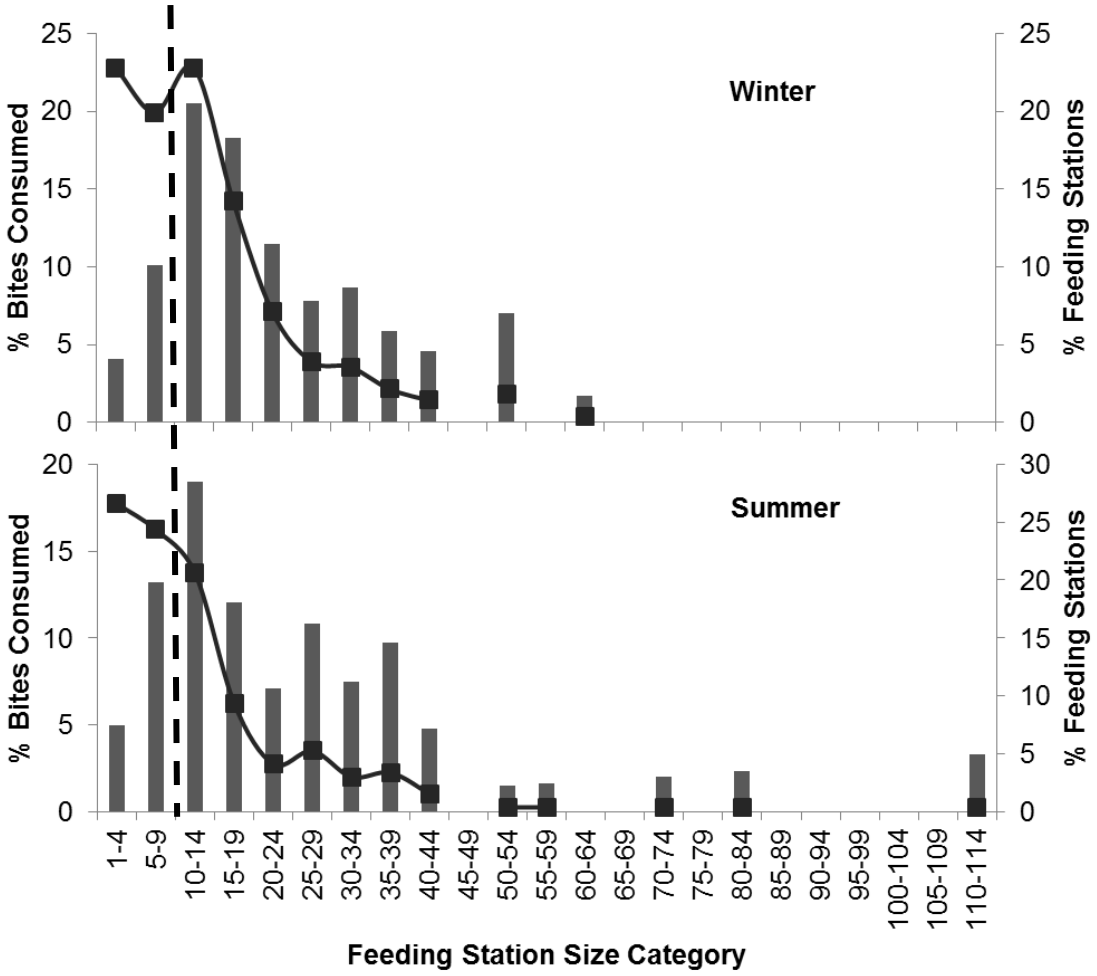

Fig. 1.3. The percent of random feeding stations measured in each size category (line) and the percent of bites consumed at all feeding stations of a given size category (bar) in winter and summer. The dashed line separates the small feeding stations (≤9 bites) from the large feeding stations. In winter, 57% of the random feeding stations were considered large but they accounted for 86% of the consumed bites. In summer, 49% of the random feeding stations were considered large but they accounted for 82% of the consumed bites.

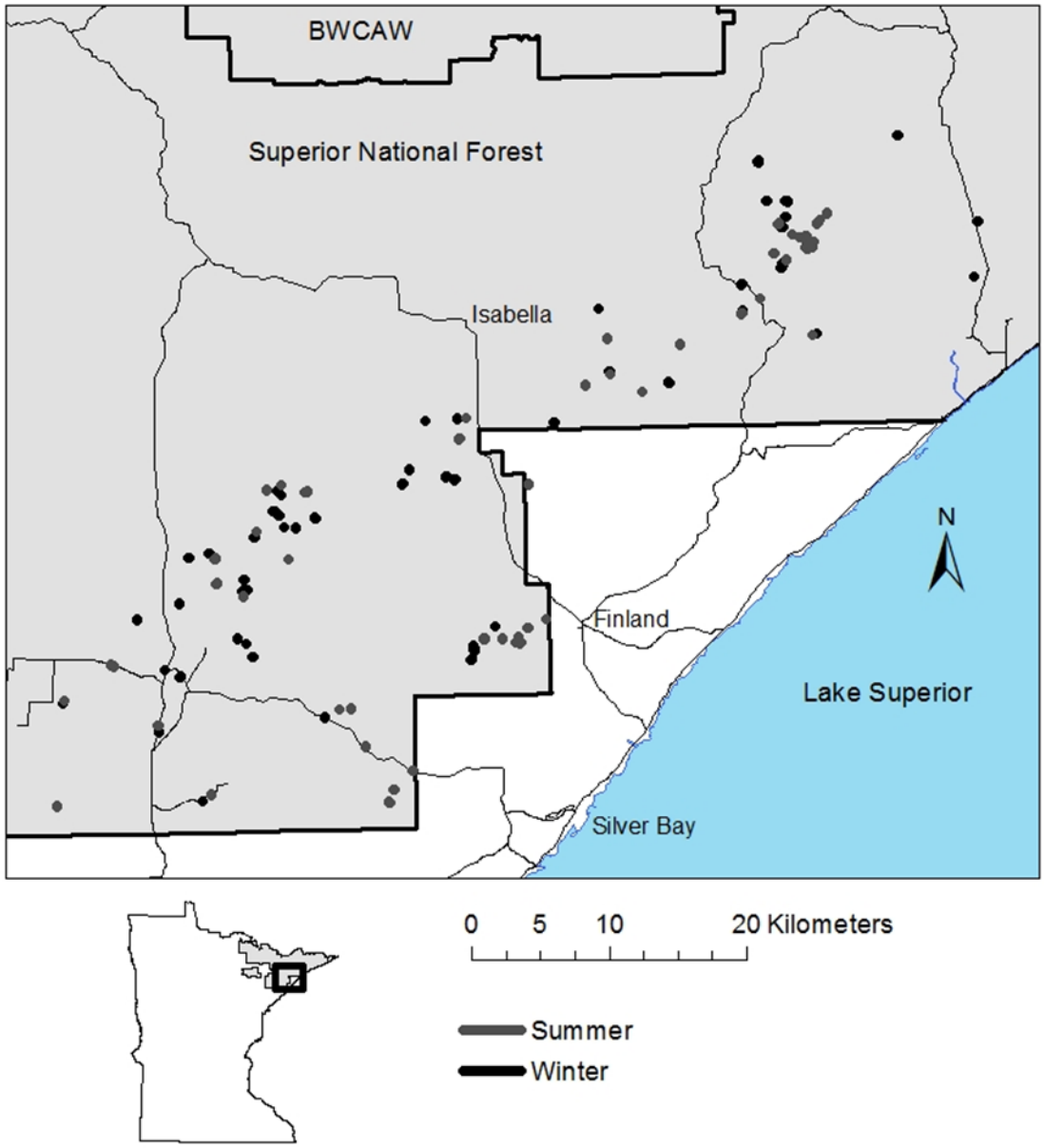

Fig. 2.1. The study area and locations of foraging paths and regenerating stands in the Superior National Forest in northeastern Minnesota. The locations spanned from Langley River Road in the southwest up to Sawbill Trail in the northeast. Each black dot represents one measured foraging path or regenerating stand measured in winter and a dark gray dot represents a summer foraging path or regenerating stand.

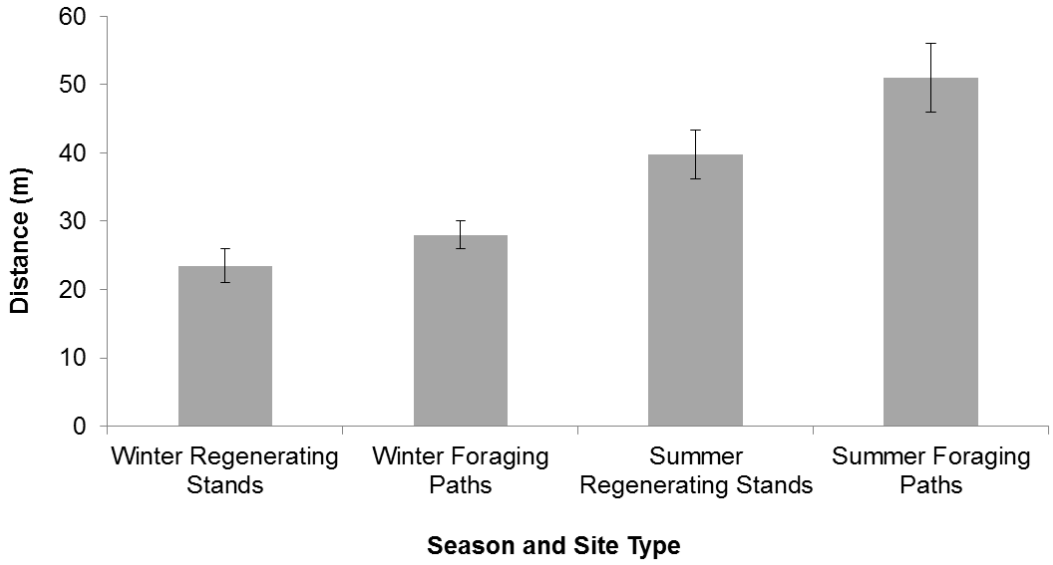

Fig 2.2. The mean distance (m) moved to complete ten large feeding stations at regenerating stands and foraging paths in winter and summer.

(a)

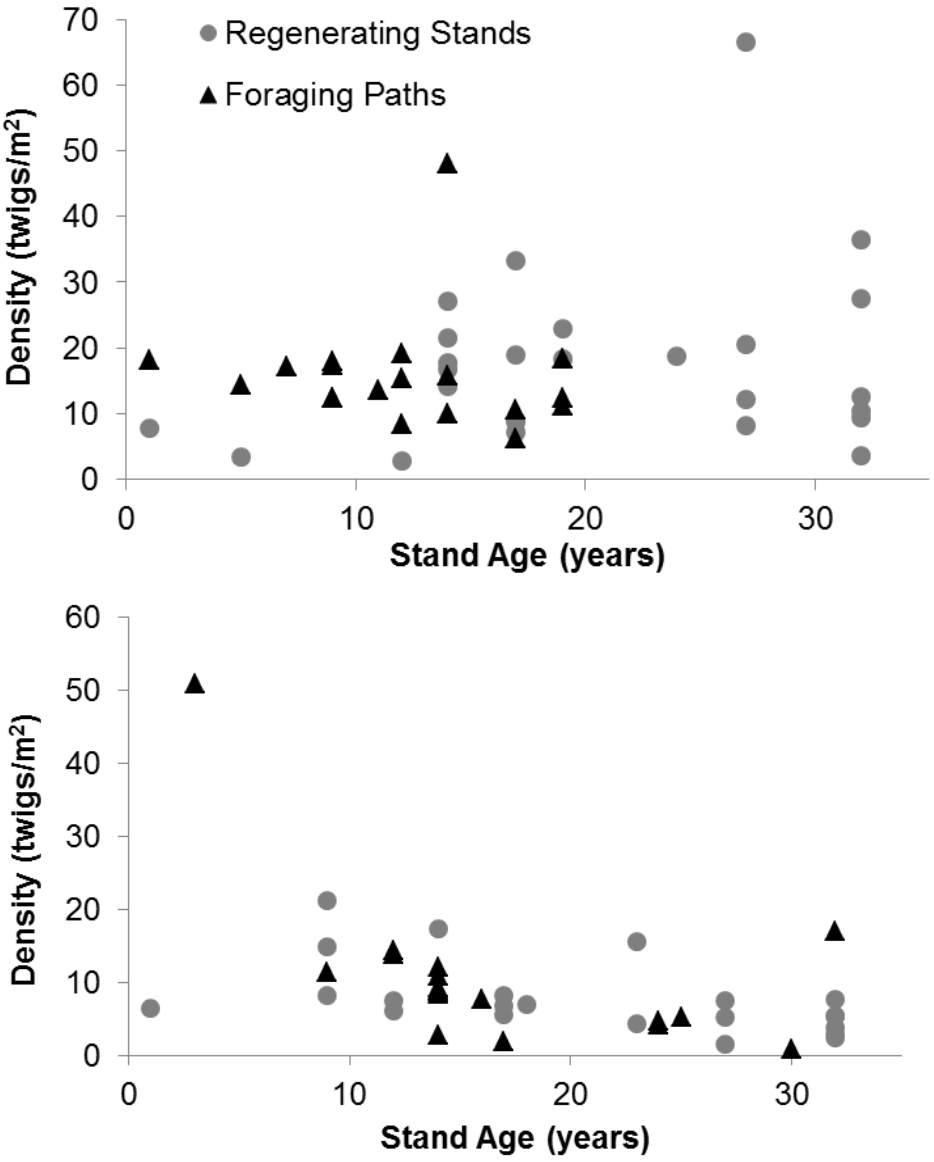

Fig. 2.3. Relationship between browse density as stands mature after forest harvest in (a) winter and (b) summer.

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